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MORPHOLOGICAL AND GENETICAL STUDIES OF FATUOID AND OTHER ABERRANT GRAIN-TYPES IN *AVENA*.

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(With Two Plates.)

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In the course of investigations relating to the production of new and improved varieties of oats at the Welsh Plant-Breeding Station, Aberystwyth, large numbers of hybrid plants, the offspring of artificially produced crosses, and pure line plants of a number of varieties and species of oats have been studied by the writer. Although primarily investigated in relation to certain prescribed characters of economic or systematic value, search at the same time was made for the appearance of individuals possessing mutant characters, such as those of the false wild oats, and for unusual characters or character combinations.

In the examination of material of this kind the occasional appearance of fatuoids or false wild oats was to be anticipated. Such forms have generally been observed by most investigators engaged in the study of cultivated varieties of oats. They are of general occurrence in the majority of the varieties of the species *Avena sativa* L., and are found also in certain varieties of the species *A. sterilis culta* (Marquand).

A certain number of individuals, however, were found which showed slight deviations in awn development, pubescence and articulation from the true false wild type, and also one form which showed differences in spikelet number in association with fatuoid grain characters. Details of the occurrence, morphology and genetical behaviour of these several kinds are the subject of the present paper.

I. FATUOIDS OR FALSE WILD OATS: GENERAL CHARACTERISTICS.

The common fatuoid differs from the normal plant of the variety in which it occurs in three main characters of the grain, namely, in articulation, pubescence, and awn development. All grains of the spikelet, primary, secondary and tertiary, are characterised by the presence of a horseshoe-shaped articulation at the base, in the form of a "sucker-mouth," the development of which causes the grain to shed readily when ripe. The callus forming the horseshoe prominence is fringed laterally and dorsally with dense, tufted pubescence, forming a kind of pappus; the rachilla is densely pubescent and a strong, twisted and geniculate awn is invariably present on all grains of the spikelets (see Plate I, figs. 11 and 15; also Plate II, fig. 22 (*d*)). In other morphological characters, both vegetative and reproductive, fatuoids are identical with the varieties in which they arise. The three main distinguishing features of the fatuoid grain have been found to behave in inheritance as a completely linked group. When crossed with grain of normal type (see Plate I, fig. 12 and Plate II, fig. 22 (*c*)) the F_2 segregates fall into three classes or genotypes, namely, homozygous fatuoid, heterozygous fatuoid and homozygous

normal, and these generally occur in the numerical ratio of 1 : 2 : 1 respectively. Genetically, therefore, fatuoids differ from normals by a single factor, or by a completely linked group of factors.

II. THE LITERATURE OF THE SUBJECT AND GENERAL REVIEW.

Since our knowledge of fatuoids has recently been reviewed by Huskins and Fryer (12) and also by Stanton, Coffman and Wiebe (20), only a few of the chief points will be considered here.

Most of the literature dealing with fatuoids relates to their occurrence, their characteristic deviation from the normal, and the general mode of inheritance of the deviating characters. Investigators in general are agreed that fatuoids occur, initially, in the heterozygous form, and that the fully developed fatuoid does not appear until the following generation. Marquand (17) obtained a fatuoid which arose at once as a fully developed homozygous individual, but this appears to be an exceptional mode of occurrence.

Opinions differ widely as to the cause of the sudden appearance of heterozygous fatuoids, and the problem of their "mode of origin" has been, and continues to be, the main point of controversy and investigation.

The agreement in articulation, pubescence and awn character between fatuoids and the true wild oat, *A. fatua*, and the similarity in breeding behaviour in respect of these characters when the two kinds are crossed with normal, or cultivated oats, are interpreted by Tschermak (22, 23), Zade (26), Crépin (3, 4, 5) and others as an indication of the origin of fatuoids by natural crossing between the cultivated varieties and *A. fatua*.

Nilsson-Ehle (18), however, disagrees with this interpretation, and maintains that fatuoids arise by a change within the mother plant itself, namely, by complex gene mutation in one of the germ cells; and this view until recently has received fairly general support.

More recently, however, a new hypothesis, based upon evidence of a cytological and genetical character, has been advanced by Huskins (14, 15), who found that fatuoids arise "neither by crossing between *A. sativa* and *A. fatua*, nor by gene mutation as previous writers have believed, but by chromosome aberration." On this hypothesis the common heterozygous fatuoid originates by the loss of the "normal" or "*sativa*" chromosome, and of its substitution by a supernumerary "*fatua*" or "fatuoid" chromosome in one of the germ cells—the actual chromosome numbers remaining unchanged.

In addition to the common fatuoid type, Huskins investigated two

exceptional strains which differed in breeding behaviour and other features from the common type. In these two strains the segregation ratio was highly variable, and in different daughter progenies ranged from 1 : 1 : very few, to 1 : 10 : very few, normal : intermediate : fatuoid respectively. In both strains the fatuoids were dwarf and sterile, as well as few in number.

These two exceptional strains were of separate varietal origin. One arose in a head selection plot of Victory oats (*A. sativa*), and the other in a plot of the variety Kanota (*A. sterilis culta*). In both cases the initial and subsequent heterozygotes were similar in vigour and external characters to common heterozygous fatuoids.

From cytological studies of both the common and exceptional types Huskins defined three series or groups of fatuoids—which he termed *A*, *B* and *C* series respectively—the main characteristics of which are as follows:

A series. Segregation occurs in the approximate ratio of 1 : 2 : 1, all segregates are of equal vigour and normal chromosome complement ($2n - 42$), but pairing of the chromosomes in meiosis is less regular than in normal *A. sativa* varieties.

B series. The segregate classes appear in ratios varying from 1 : 5 to 1 : 10 normals and heterozygotes respectively, plus a few sterile and dwarf fatuoids. The normals, heterozygotes and fatuoids respectively possess 42, 41 and 40 chromosomes, and cytological conditions are extremely irregular.

C series. These give ratios of 1 normal to 1 heterozygote plus a few sterile and dwarf fatuoids; occasionally give ratios of 1 : 2 : 1. The fatuoids have 44 chromosomes, normals 42 and heterozygotes 43. Meiotic divisions are very irregular.

The great majority of fatuoids belong to the *A* series group, for only three examples are on record of the occurrence of individuals showing chromosome deviations, abnormal segregation, dwarfness and sterility typical of the *B* and *C* series types. Two of these are those described by Huskins (14) and already referred to above, whilst the third was obtained by Goulden (10) in the variety Banner. In this particular strain fatuoids and heterozygous fatuoids segregated in about equal numbers, while only a few normals appeared. The fatuoids were dwarf and sterile, but the members of the two other classes were normal in fertility and stature. This fatuoid type differs rather strikingly in its class ratios from those studied by Huskins, and in this respect does not conform fully to either the *B* or *C* series groups.

Stanton, Coffman and Wiebe (20), from a study of the mode of occurrence and genetics of a number of fatuoid forms, all apparently of the *A* series type and belonging to distinct varietal strains, also conclude that fatuoids arise by chromosome aberration. They maintain that the fatuoids which occur in Fulghum and Burt (varieties of *A. sterilis culta*) differ genetically from those occurring in varieties of the species *A. sativa*.

There are therefore three main hypotheses in explanation of the mode of origin of the *A* series fatuoids, namely:

(1) Natural crossing.

(2) Complex gene mutation.

(3) Chromosome aberration.

The latter hypothesis also applies to fatuoids of the *B* and *C* series groups.

III. MATERIAL AND METHODS.

The present survey relates to spaced plants, plant rows and commercial plots of oats grown at the Welsh Plant-Breeding Station, Aberystwyth, during the years 1923–7. Most of the aberrant types discussed in this paper were discovered by the writer in hybrid generations derived from artificial crosses between varieties of *A. sativa* and strains of the species *A. sterilis culta* and *A. nuda*. Some were obtained in plots of commercial oats, of both foreign and native strains, more than a hundred varieties of which were grown and examined during each of three successive growing seasons. For some of the specimens, however, the writer is indebted to Mr Martin G. Jones[1].

When mutant plants were observed in the field, search was made within the plot or family group for any other abnormal plants which might be present. At harvest time the aberrant plants were removed individually, their number recorded and notes taken on their particular grain characters. The following year the seeds from each individual plant were sown in beds, generally in a bird-proof cage, the individual grains being spaced at regular intervals. Seeds of the normal strain were sown on a similar plan alongside, when necessary for comparative study. In some cases, however, the seeds were not spaced but were distributed uniformly in short plant rows: this practice was adopted in some of the earlier studies.

Where the mutant types were obtained in threshed samples of grain, the aberrant individuals were removed singly and sown as spaced grains; and if both heterozygous and homozygous mutant grains were present,

[1] Formerly agronomist, Welsh Plant-Breeding Station, now of Imperial Chemical Industries Limited.

and distinguishable, a grouping on this basis was made before the individual seeds were sown.

Artificial hybridisations between the respective strains were carried out in a cool greenhouse. Of the individual plants used for crossing, at least one good tiller was allowed to ripen to provide seed from which to raise line progenies for later comparison with the hybrid generations.

In the earlier investigations of the F_2 and F_3 material of the artificial hybrids the seeds were sown *in situ*, but this procedure, owing to various pests attacking the young seedlings, frequently resulted in heavy casualties and in irregular plant establishments. In most of the later studies, therefore, and whenever number and length of culms and spikelet numbers were being critically studied, the F_2 seeds were sown in boxes in a greenhouse, and the seedlings later planted out at uniform spacings in a bird-proof cage. This procedure, while more laborious, gave satisfactory plant establishment.

Inheritance studies with fatuoids, and also with certain of the strongly awned types, give rise to practical difficulties owing to the ease with which the grains shed when ripe. With adverse weather conditions at the time when the plants are approaching maturity it was a frequent experience to find much, if not all, of the grain lost through shedding. In such instances, the growing of F_3 families and line progenies of the homozygous mutant segregates in adequate numbers for genetical requirements was a matter of much difficulty, and often of practical impossibility.

IV. ABERRANT GRAIN TYPES: THEIR OCCURRENCE AND GENERAL MORPHOLOGY.

(*a*) FATUOIDS IN ESTABLISHED VARIETIES.

Nine varietal strains of fatuoids met with appeared in established varieties of oats. Five were observed in the year 1923 in the varieties Fulghum, Orion, Ceirch-du-bach and Royne; one the same year in the species *A. nuda*; one in 1926 in the variety Cornellian, and two in 1927 in the varieties Golden Giant and Record respectively. With the exception of Fulghum (*A. sterilis culta*), Golden Giant (*A. sativa orientalis*) and *A. nuda*, all the strains belong to the species *A. sativa*.

The Orion, Ceirch-du-bach, Scotch Potato and Royne fatuoids were discovered as individual grains in threshed samples obtained from experimental plots of these varieties which had been grown from seed of the ordinary commercial kind.

The fatuoids of Fulghum, Cornellian, Golden Giant and Record, on

the other hand, were first observed in plots growing in the field. In each instance only single plant specimens were obtained—except in the case of Fulghum, of which single specimens were found in each of two beds during the same growing season. Although careful search was made in the beds in which the fatuoids were observed, no plants of the heterozygous type could on any occasion be found.

The fatuoid of *A. nuda* occurred in the line progeny of one of a few plants of this species which had been grown in pots the previous season for hybridisation purposes. The offspring of this particular individual showed segregation for the characters hulled and hull-less, fatuoid and non-fatuoid, and for black, grey and white colour of grain. Such complex segregation at once distinguished this type from all the others and pointed to its possible occurrence through natural crossing, probably by stray pollen from some black-grained fatuoid plant.

The fatuoid of Golden Giant, however, is of special interest, owing to the fact that the type variety, unlike the type varieties of the other strains, possesses a panicle of unilateral character and leaves which are all eligulate, characters which contrast strongly with the spreading panicle and ligulate leaves, characteristic of the wild oat, *A. fatua*. The Golden Giant fatuoid nevertheless agreed with its parent stock in being unilateral and eligulate. The grain of this form is fully yellow in colour as in the type variety[1].

Of the several fatuoids considered above, all except *A. nuda* differ from the parent strains only in articulation, pubescence and awn development; whilst in vigour, as judged by height of plant, they appear to be in every way similar to their respective normal stocks. In so far as these attributes are concerned, these several fatuoid strains agree with typical *A* series fatuoids[2]. They are, however, divisible into two classes, or types, on the basis of the length of the pubescence on the callus. In Fulghum, Orion, Ceirch-du-bach, Scotch Potato, Royne and *A. nuda* the basal hairs are long, from 3–4 mm., whilst in Cornellian, Golden Giant and Record the hairs are distinctly short, being only 1 mm. or less in length (see Plate I and compare figs. 14 and 15). These differences, as will be shown later, are due to a factor modifying length of pubescence which is inherited independently of the fatuoid complex.

In general characteristics, however, all these fatuoids are of the

[1] In this respect it differs from the fatuoid of the yellow-grained variety Golden Rain, previously described by the writer (16), in which the yellow colour is practically completely absent from the grain of the heterozygous and homozygous phenotypes, and appears only in the normal segregates.

[2] Huskins' classification (15).

common, or *A* series, type. Further investigations and detailed and comparative studies of length and number of culms, number of spikelets per plant, and other plant characters have been made with normal and fatuoid plants of the variety Fulghum. These data are recorded and discussed in a separate section below (see pp. 28–34). Similar investigations are in progress on the fatuoids and normals of the varieties Orion, Cornellian and Scotch Potato respectively; the observations relating to these will be published in a later paper.

(*b*) Fatuoids in artificial hybrids.

Several homozygous fatuoids, apparently of the *A* series group, were found in the progeny of various artificial crosses. They occurred in one F_3 family of the cross President (*A. sativa*) × Pioneer (*A. sativa orientalis*); in two F_3 families of Victory (*A. sativa*) × Red Algerian (*A. sterilis culta*); and in F_3, F_4 and F_7 families of crosses between Red Algerian and Scotch Potato (*A. sativa*). It will be observed that all, except the first named, are inter-specific crosses between varieties of the species *A. sativa* and *A. sterilis culta*.

In all these examples, however, heterozygous fatuoids were present in conjunction with the homozygotes when these were first observed to occur. This point is important in that it would seem to indicate the occurrence of the initial aberrant plant as a heterozygote in the generation immediately preceding that in which the homozygous fatuoids appeared. Such a view receives additional support from the fact that the families in which the fully-formed fatuoids occurred were comprised of fatuoid, intermediate and normal plants in numbers approximating to a simple Mendelian ratio.

When heterozygous fatuoids arise in segregate material it is often very difficult, and occasionally impossible, to decide whether such forms have, or have not, arisen by cross-pollination with some fatuoid in the immediate vicinity of the hybrid. In contrast to fatuoids arising in pure line varieties, the general similarity of the fatuoid to the parent stock in respect of non-fatuoid characters does not here obtain, for the mother plant is frequently already heterozygous to a greater or less degree. When, however, other plant characters of an unexpected kind appear in conjunction with the fatuoid characters, the possibility of their simultaneous introduction through natural crossing, rather than by any inherent germinal change within the mother plant itself, has to be borne in mind.

That certain of the fatuoids mentioned above were the outcome of natural crossing is suggested by the fact that in F_2 *ex* Victory × Red

Algerian (white- and buff-grained varieties respectively) three out of 300 segregates had grain which was black in colour. Black being dominant both to white and to buff, these three plants were at once suspected of being natural hybrids. In the next generation it was found that they segregated for colour of grain into black and non-black phenotypes in approximately three of the former to one of the latter, and, moreover, in two of the progenies there also occurred segregation into fatuoids, intermediates and normals. It is clear, therefore, that in these two instances the mother plants were hybrid for both black colour and fatuoid type of grain, and that very probably the factors for both these characters were simultaneously introduced by chance cross-pollination of the F_1 mother plant with pollen from some black-grained fatuoid oat. The occurrence of black-grained F_1 plants of the cross Sir Douglas Haig fatuoid × normal growing near-by suggests that these three aberrant individuals probably originated by natural crossing through stray pollen from this source.

The origin of the other fatuoids, however, cannot be attributed to the same cause. In general, they appeared to differ from their sister segregates only in the occurrence of the fatuoid or heterozygous fatuoid characters of the grain.

In the case of the fatuoid which occurred in the F_7 family of Red Algerian × Scotch Potato, the mother plant was true-breeding in relation to size, colour and general characters of the grain and for equilateral type of panicle, and the fatuoid resembled the parent plant in all these features.

In respect of the other examples (all white-grained fatuoid forms) no fatuoids possessing white colour of grain, or hybrid for white grain colour, were present in the neighbourhood of the mother plants from which these forms arise; it is, therefore, difficult to see how natural crossing could in any way have been responsible for the origin or occurrence of these.

Hence, while some of the above-mentioned fatuoids arose through natural crossing with other fatuoid plants, the majority have probably arisen by some change within, rather than without, the mother plant; for in practically all cases they show close agreement with the general characteristics of the mother plant stocks.

(c) A "SUB-FATUOID" TYPE.

In 1924 five plants which possessed promising economic characters were selected from an F_3 family (265 Cn 199)[1] *ex* Red Algerian × Golden Rain. The following spring, seed from each of these was sown in separate plant rows for further study. When harvested, and later analysed in the

[1] Station reference symbols.

laboratory, one of the plant rows was found to consist of 14 panicles bearing grain of a peculiar "sub-fatuoid" or "semi-steriloid" type, and 36 panicles bearing grain of either normal or intermediate type. The other plant rows contained only plants bearing normal grain similar to that possessed by the original selected mother plants. No differences in grain characters had been noted between the five original mother plant selections.

The spikelet and grain features of this new form are illustrated in Plate II, fig. 21 (*b*) and Plate I, figs. 1–5, where it will be seen that the *spikelet* articulation (see Plate I, fig. 1) closely resembles that common to *A* series fatuoids, but the articulation of the floret differs in a marked and characteristic manner. On casual examination the ripe spikelet, with its closely adhering secondary and tertiary grains, appears to resemble a true steriloid: but when the individual grains are closely examined and pulled apart, the apex of the rachilla on its inner side is seen to possess an oblique cleavage plane of the fatuoid type which, however, is only partially developed (see Plate I, fig. 4). This latter feature causes the floret to remain adherent in the spikelet and prevents the secondary and tertiary grains from falling apart when mature, thus producing a false steriloid type of spikelet. By applying slight bending pressure to the rachilla, a fracture generally occurs in the region of the partially developed cleavage plane, and a partially developed "horse-shoe" articulation, with its characteristic cavity, comes into view (see Plate I, fig. 5). This kind of floret conjunction is characteristic of all the upper grains of the spikelet, whether the latter consists of two, three or more grains.

In the spikelets of some panicles, however, the pulling apart, by hand, of the secondary grains results in the fracture of the rachilla at its base, as in *A. sterilis culta* (see Plate I, fig. 1). In these, however, the cleavage plane is more rudimentary. From inspection of a large number of grains, slight fluctuating variations in the degree of development of the cleavage surface have been noticed, but no examples have been found in which the cleavage has developed to the extent characteristic of the true fatuoid grain, nor, on the other hand, is the cleavage plane ever entirely missing.

As in typical fatuoid oats the basal callus and rachilla carry dense pubescence, that on the rachilla being medium long (1–3 mm.), whilst that on the callus is short (about 1 mm.). The occurrence of a fully developed horseshoe-shaped articulation at the base of the primary grain, however, causes the spikelets of this oat, like those of the common fatuoid, to shed freely when ripe.

The occurrence of partial articulation surfaces or planes of cleavage at the apices of the rachillae, and of a strong, twisted and geniculate awn on all grains of the spikelet, indicate a closer affinity to a fatuoid than to a "steriloid" type of grain; for these reasons this mutant form has been designated "sub-fatuoid" rather than "sub-steriloid," or "steriloid."

Initial breeding study. In 1926, seeds of all the normal and the intermediate, and of one of the sub-fatuoid panicles of the abnormal plant row were sown in a field in separate panicle rows. Germinations were extremely poor, as judged by the number of seedlings which appeared above ground, and during the early part of the growing season the already poor establishment was much reduced by a bad attack of wireworm. A small number of panicles were eventually harvested from the few scattered plants which survived, but no panicle rows contained sufficient plants to permit of the collection of data with regard to the breeding behaviour of the different sorts of panicle.

The same season, two small lots of sub-fatuoid grain, sown for hybridisation purposes in pots in a cool greenhouse, gave good germination and vigorous plants. These all bred true for the fully developed sub-fatuoid type of grain.

In 1927, 97 plants were raised from the collective seed of three of the sub-fatuoid plants grown in the greenhouse the previous season, and these all gave grain of the homozygous sub-fatuoid type.

The apparently true-breeding behaviour of the plants bearing the sub-fatuoid kind of grain, and the occurrence of homozygous sub-fatuoid panicles in approximately simple recessive numbers in the original F_4 family, indicate that the sub-fatuoid oat, like the *A* series fatuoid, is probably a simple homozygous recessive in relation to the normal or cultivated oat. In order to test this point, hybridisations between sub-fatuoid and normal plants were made in 1927. The same year the sub-fatuoid was also crossed with a fatuoid of a typical *A* series kind[1].

A plant with spikelets very similar to the sub-fatuoid described above has been found by Stanton, Coffman and Wiebe (20) in the variety Sixty Day (*A. sativa*). This form, they report, "differed markedly from the normal fatuoid, in that its seeds were not dropped immediately on ripening and a decided tendency existed in many spikelets for the florets to remain together in threshing as is true with derivatives of *Avena sterilis*."

This strain is stated by them to be intermediate between *A. fatua* and *A. sterilis*, but as the minute details of floret adherence and disjunction

[1] The inheritance data relating to the F_1 and later generations of these two crosses, which are not yet complete, will be published in a later paper.

are not given, a critical comparison of the two strains cannot here be made. From the published data and photograph, however, the two forms appear to have certain features in common.

(*d*) Various strongly awned types.

Four distinct types of strongly awned mutants have been discovered in the course of this study. For convenience of reference and investigation these have been designated Types A, B, C and D respectively. The details of these are as follows:

Type A ex A. sativa *var. Ceirch-du-bach.*

In 1923, a grain sample of an L_3 generation of Ceirch-du-bach oats was found to contain a number of grains with strong, twisted and geniculate awns and dense basal pubescence. These abnormal grain types were brought to my notice by Mr M. G. Jones, under whose supervision the strain had been developed. On casual observation the aberrant grains appeared to resemble fatuoids, but on close examination it was seen that they differed by the absence of a definite horseshoe-shaped callus formation at the base of the grain (see Plate I, fig. 13, and compare with fig. 11).

In the roughly threshed sample there were a number of two-grained spikelets, with the upper and lower grains still remaining intact; from amongst these it was possible to distinguish three main kinds of spikelets:

(1) Those with both upper and lower grains bearing strong, twisted and geniculate awns;

(2) Those with a strong, twisted sub-geniculate awn on the lower grain, but with the upper awnless, and

(3) Those with both upper and lower grains awnless[1] (spikelets of these three types are shown in Plate II, figs. 20 (*a*), (*b*) and (*c*) respectively).

By analogy with fatuoids these three kinds should represent respectively the homozygous mutant, the intermediate and the normal or type strain.

In addition to these differences in awn development, associated differences in the degree of solidification and pubescence of the base of the lower grain, and in the amount of pubescence on the rachilla were to be seen. For example, in (1) a large oval-shaped cavity occurs at the base of the lower grain—giving rise to an articulation surface which effects early release and shedding of the spikelet when ripe; also fairly

[1] Members of this class were later found to give rise to panicles in which an occasional lower grain possessed a rather small and slightly twisted awn.

dense tufts of moderately long (2–3 mm.) brownish hairs occur laterally, at the base, and hairs are also present on the rachilla (see Plate I, fig. 13). In (2) the basal cavity is much reduced in size, and pubescence is reduced to very small lateral tufts and to just a few hairs on the rachilla; whilst in (3) complete solidification and practically no pubescence characterise the grain (see Plate I, fig. 12).

In all three kinds of spikelets the *base* of the *upper* grain is glabrous and solidified, and identical with that of the normal or type strain. The upper grains of group (1), however, are characterised by the presence of a strong, twisted and geniculate awn.

Floret separation in all three classes is of the *A. sativa* type.

On referring to the descriptive notes of the "head selection" from which this segregating line was originally developed, and upon seed samples of the descendant generations, it was found that similar mutant and intermediate types of grain were present in the progeny derived from the initial head selection, the grain of which was described as being "black, long and slightly awned." It appears, therefore, that this strain of Ceirch-du-bach originated from a plant which, when selected, was heterozygous for the mutant characters in question.

Of the 60 individual heads originally selected for the isolation and development of pure line strains of this variety, all except the strain under review gave progenies true to type and homozygous for all external plant characters.

Initial breeding tests. In the spring of 1923 preliminary breeding tests of the three kinds of spikelets described above were commenced. Thirteen two-grained spikelets representing the three classes were taken, and the individual grains sown singly in a bird-proof cage.

Eight spikelets of class (1) gave 15 plants of class (1) type; one grain failed to germinate.

Two spikelets of class (2) gave two plants of class (2) and one plant of class (1) type; one plant owing to insect injury failed to produce panicles.

Three spikelets of class (3) gave nothing but class (3) type of plants.

From the initial studies it appears that the two-awned spikelets represent the homozygous mutant genotype, the single awned the heterozygous mutant, and the awnless the homozygous normal or type strain. This conclusion was later verified by growing complete progenies from representative plants of the three groups in the following season.

In external appearance the spikelets of the intermediate or heterozygous class are practically indistinguishable from those of the heterozygous fatuoid of this variety.

In order to study the relationship of the Type A mutant to the fatuoid oat, reciprocal crosses were made between it and fatuoids, both of the black-grained variety Supreme and of the white-grained variety Scotch Potato.

The Type A form has also been crossed with a fatuoid of the type variety (Ceirch-du-bach).

The genetical data relating to these crosses are recorded and discussed under "Hybridisation data" below (see pp. 40–47).

Type B ex F_3 *family of Red Algerian* × *Scotch Potato* (A. sterilis culta × A. sativa).

Another strongly awned mutant referred to as Type B, which is very similar to Type A described above, appeared in an F_5 family of the cross Red Algerian × Scotch Potato. This form, however, differs from Type A in one very marked and important taxonomic feature, namely, in that the rachilla, after threshing, remains firmly attached to the apically adjacent grain and not to the subjacent grain. Floret separation in Type B, therefore, is of the *A. sterilis culta* kind.

Compared with Type A the pubescence on the rachilla is denser and more abundant, and in this respect Type B shows close affinity to typical fatuoid pubescence.

Apart from these features of the rachilla, Type B is practically indistinguishable from Type A. It possesses strong, twisted and geniculate awns on both primary and secondary grains—the third grains when present being awnless—has dense tufts of medium long hairs at the sides of the oval-shaped cavity at the base of the lower grains, and the spikelets shed readily when ripe (see Plate I, figs. 6–9, and Plate II, fig. 21 (*c*), *left*).

This form first appeared in the progeny of one of a number of F_4 panicle selections of the cross Red Algerian × Scotch Potato, which had been grown on a panicle-to-row basis in 1925. The total progeny of this one particular culture comprised 21 panicles; 12 of which had spikelets in which both upper and lower grains were strongly awned with spikelet articulation only partially solidified (leaving a cup-like cavity at the base of the lower grain), and with dense pubescence at the base of the first grain and on the rachilla; six had spikelets in which the lower grains were fairly strongly awned whilst the upper were awnless, pubescence and articulation being of an intermediate character; whilst the three remaining panicles had occasional lower grains weakly awned and the upper awnless. In the latter group the rachillae were glabrous, the lower grains

possessed very few or no basal hairs, and the basal articulations were more or less completely solidified. On analogy with fatuoids and with Type A these three groups should represent the homozygous mutant, the heterozygote and the homozygous normal respectively.

In all three groups the upper grains of the spikelets are firmly attached to the lower, and floret or grain separation is in all cases brought about by fracture of the rachilla at, or near, its base.

Initial breeding tests. In 1926 separate panicle rows were sown with seed from the nine heterozygous and normal panicles, and from four of the homozygous mutant type. Very poor germinations were obtained, few seedlings appearing above ground, and wireworm attacks further reduced the seedling establishment. It was impossible, therefore, to obtain the requisite data on the breeding behaviour of the different panicle types. Many of the surviving plants produced grain which was badly filled or failed to produce caryopses, although the paleae were normally developed. This was particularly noticeable in panicles possessing grain of the mutant type. Badly filled grains also occurred, but to a lesser extent, in the panicles of both intermediate and normal plants.

A further generation of the fully awned individuals was raised in 1927. Seed from a number of the 1926 plants was pooled and divided into lower and upper grains; 41 lower and 40 upper grains were dehusked and the caryopses sown in separate boxes and placed to germinate in a large cool greenhouse.

The lower grains produced 40 seedlings; one of these appeared weakly at first, but later developed in a normal manner. The one seed which failed to germinate was found, when dug up, to be soft, milky and disintegrating and exhibited no evidence of growth.

Of the 40 upper grains 36 produced seedlings of uniform size and vigour, two gave small or weakly seedlings and two showed no signs of emerging through the soil. Of the latter, one nearly 4 weeks after sowing possessed a healthy caryopsis, but there were no signs of growth: the other, which was shrivelled, possessed small, very fine, thread-like rootlets at its base, but no shoot. No further development followed in the case of either of these seeds.

Of the two small and weakly seedlings one died before its first leaf emerged fully from the coleoptile sheath, whilst the other continued to remain small and weakly. At the time when the normally vigorous seedlings were planted out into the cage, this weakly individual was transferred to a large pot and allowed to remain in a cool greenhouse throughout the growing season. Although growing very slowly at first, five

slender tillers were eventually produced, having panicles bearing a small number of grains of the homozygous mutant type[1].

The seedlings transferred to the cage all gave rise to plants of normal stature, and all possessed the fully developed mutant kind of grain. Several, however, gave rather poorly filled and occasionally empty grains[2].

In respect of the inheritance of the mutant characters all plants grown from fully awned grains invariably gave progeny possessing only the fully awned type of grain. As in Type A, the plants with fully awned spikelets represent the true breeding mutant genotype.

In 1926 the Type B mutant was reciprocally crossed with the sub-fatuoid oat described above (pp. 9–11), and also with plants of the cultivated variety Golden Rain (*A. sativa*). Studies relating to the hybrid generations of these are still in progress.

Type C ex *Red Rustproof* × *Scotch Potato.*

This form was found in 1925 as a single segregate plant in F_2 *ex A. sterilis culta* var. Red Algerian × *A. sativa* var. Scotch Potato.

The spikelets are unlike those of either parent, and are very similar to the common heterozygous fatuoid; but the awn on the lower grain is more strongly developed and is fully geniculate. The basal articulation of the lower grain is intermediate in character, but rather less solidified than in the common heterozygous fatuoid. Basal pubescence consists of two small lateral tufts of brownish hairs varying in length from 2–5 mm. The rachilla is completely glabrous, and the second grain, which is awnless, has a slight tendency to adhere to the lower as in members of *A. sterilis*. The spikelets exhibit a tendency to shed when the ripened panicles are roughly handled (see Plate II, fig. 22 (*b*)).

This form has bred true during two further generations.

Type D ex A. sativa *var. Norwegian Grey Oat.*

The form designated Type D was isolated from a sample of Norwegian Grey oats. The lower grain bears strong, twisted and geniculate awns, but while the upper grains in some of the spikelets are awnless, others bear strong, twisted and geniculate awns (see Plate II, fig. 22 (*c*)). The base of the lower grain is solidified and glabrous, or a few hairs 2–3 mm. in length may be present (see Plate I, fig. 10). The rachilla is

[1] The following season seeds taken from this weakly plant gave rise to seedlings of normal vigour which produced mature plants all of normal size.

[2] That is, grains in which the paleae were normally developed but in which no caryopses were present.

glabrous and the upper grain separates from the lower in a characteristic *A. sativa* manner. The particular interest of this form to the present study lies in the occurrence of strong, twisted and geniculate awns in conjunction with a normal or solidified and practically glabrous type of base. In preliminary breeding studies this type has shown instability in the inheritance of the awns on the upper grain.

(*e*) WEAKLY AWNED TYPES.

Varieties with grains bearing weak, slender, non-twisted awns which are not geniculate are of fairly frequent occurrence in varieties of the species *A. sterilis culta* (Marquand). In Red Algerian, and also in certain strains of Red Rustproof, both lower and upper grains normally bear weak, slender, non-twisted awns (see Plate II, fig. 22 (*a*)). In the lower grain of these varieties the base is partially solidified, and the basal hairs moderately numerous and usually from 3–6 mm. long. The spikelets generally do not shed freely when ripe. When these varieties are crossed with certain members of the *A. sativa* species, this type of basal pubescence and articulation segregates in numbers approximating to a simple recessive class.

It has been observed that some members of this class shed their spikelets more readily than is the case with typical *A. sterilis culta* forms. The pubescence at the base of these divergent individuals is somewhat denser than that of the parent strains, the base of the grain is less solidified and shows when shed a moderately large oval-shaped cavity, which is strikingly similar to that present in the Type A and Type B forms described above. In these aberrant *A. sterilis culta* forms close association exists between degree of pubescence and degree of solidification of the base of the grain, and also between these characters and the weak awn. The spikelets, however, differ from those of Type A and Type B in the more general absence of pubescence on the rachilla. Data relating to inheritance studies, in connection with crosses between *A. sativa* and *A. sterilis culta*, are given below (see pp. 48–49).

Segregates of the weakly awned type obtained from the cross Red Algerian × Scotch Potato have been crossed with plants of Type C and also with a strain of awnless oats received from Dr C. L. Huskins of the John Innes Horticultural Institute, Merton.

(*f*) VARIOUS TYPES OF PEDICEL.

Some of the different types of pedicels met with in these investigations show variations at their apices which conform to the mode of separation

of the spikelet. In those types in which the spikelet sheds freely, and the lower grains show a small cavity or sucker-mouth at the base, a small section of callus remains adherent to the apex of the pedicel. This callus appears as a disc-like prominence, and its surface of articulation forms a plane of cleavage more or less oblique to the line of axis of the pedicel (see Plate II, figs. 16, 17 and 18). When the spikelets do not shed readily, as in *A. sativa* varieties, separation occurs by fracture of the callus in a transverse direction and near its base (see Plate II, fig. 19). The close similarity in size of the adhering callus between the strongly awned and weakly awned types is shown in Plate II, figs. 17 and 18. The somewhat larger callus typical of fatuoids is shown in Fig. 16, and the smaller residues of the *A. sativa* type in Fig. 19. In general, the larger the disc of callus adhering to the pedicel, the more freely do the spikelets shed.

V. HYBRIDISATION DATA.

(*a*) Golden Rain fatuoid × Golden Rain normal[1].

Practically all of the results obtained by investigators of the fatuoid problem up to recent times have shown that the common fatuoid oat, *i.e.* the *A* series fatuoid, differs from the parent variety in which it originates by just those characters which distinguish the fatuoid grain from the normal, viz. awn development, pubescence and articulation. Some workers have, however, demonstrated slight differences in height of plant and tillering capacity between the extracted fatuoid and normal segregates, but such differences have not been of a marked character.

While investigating the inheritance of grain colour in the Golden Rain fatuoid × normal cross, however, it was observed that rather marked differences in spikelet number appeared to exist between the normal and fatuoid parent lines, and also between the segregate classes in the F_2 and F_3 generations. Differences between the progeny of the parent strains were first observed when plants of the F_1 hybrids and parental lines were grown side by side as spaced individuals in 1924. Preliminary counts made at that time on some of these showed that decided differences occurred. Later, when the F_2 generations were raised, the extracted fatuoids appeared to possess fewer spikelets per panicle than the extracted normals, thereby suggesting an association of low spikelet number with fatuoid type of grain.

The Golden Rain fatuoid nevertheless, when crossed with normal,

[1] The progeny of this cross has been previously studied by the writer (16) in connection with the behaviour of the yellow colour of the grain in relation to the fatuoid complex.

gives segregates of equal vigour, as judged by height of plants and tillering capacity, and the segregate classes appear in the numerical ratio of 1 : 2 : 1 fatuoid, intermediate and normal respectively. In respect of these characters, therefore, this fatuoid agrees closely with the general characteristics of the *A* series group as defined by Huskins (14). From the general appearance and vigour of all segregate classes, the chromosome complement is probably similar in all phenotypes, but this has not been determined.

In order to study critically the behaviour in inheritance of culm and spikelet characters in relation to type of grain, two F_2 generations were separately raised from F_1 plants (709 and 714 Cn) in 1927. Counts were also made the same year of spikelets in a number of F_3 families of 713 Cn. Line progenies (L) were grown from both fatuoid and normal parents for comparison with the hybrid offspring.

The F_1 *hybrid and* L_1 *parent generations.*

The preliminary spikelet counts made in 1924 on some of the F_1 plants and on single representative plants of the parent lines are given in Table I. It will be seen that the parent lines differ widely, the number of spikelets in the fatuoid plant being 263 and in the normal 445. The average total figure for the several panicles of the three F_1 hybrids is 473, which is slightly higher than the figure for the normal line. The plant of the fatuoid line shows low numbers of spikelets in all its panicles as compared with both the normal and the hybrid plants. These figures, however, are but single estimations, and give only a general indication of the state of affairs found in the F_1 and L_1 generation plants.

The F_2 *and* L_2 *generations.*

One hundred seeds from each of two F_1 hybrids (709 Cn and 714 Cn) and 50 seeds from each parent line were sown in boxes in a cool greenhouse. Germinations were good and only two seeds failed. When in the four-leaf stage the seedlings were planted out into a bird-proof cage and spaced at regular intervals of 6 inches apart. Both parent lines and segregates were very uniform in size and vigour, and developed into good average-size plants.

The F_2 family, 709 Cn, was lifted for investigation as soon as the panicles were fully extended and before the grain was ripe.

It was found, however, that in the unripe condition, division of the segregates into the three phenotypical classes, fatuoid, intermediate and normal, for statistical comparison could not be accurately carried out

TABLE I.

Showing number of spikelets in F_1 *hybrids and parent plants of the cross Golden Rain fatuoid × normal*—1924.

Description of F_1 hybrid and/or parent	Reference numeral	Number of spikelets per panicle: Panicle No. 1	Panicle No. 2	Panicle No. 3	Panicle No. 4	Panicle No. 5	Panicle No. 6	Panicle No. 7	Panicle No. 8	Panicle No. 9	Total no. of spikelets per plant
Golden Rain fatuoid × Golden Rain normal	710 Cn	139	81	78	72	70	68	39	—	—	547
do. do.	712 Cn	82	75	67	54	47	46	—	—	—	371
Reciprocal	714 Cn	97	81	72	63	57	43	37	27	25	502
Average of totals											473·3
Parent lines:											
Golden Rain fatuoid Plant No. 1	Cn 578/1	56	40	37	36	27	25	22	20	—	263
Golden Rain normal Plant No. 1	Cn 577/1	133	84	68	53	49	37	21	—	—	445

owing to the difficulty of distinguishing all the members of the intermediate and normal phenotypes[1]. The plants were therefore divided into fatuoid and non-fatuoid[2] groups; these were clearly defined and could be accurately determined. Spikelet and culm determinations were then investigated in relation to these two groups.

The intention, however, to study distributions in relation to the three categories fatuoid, intermediate and normal in the family 714 Cn—which was left for this purpose to grow to maturity—had to be abandoned owing to the damaged condition of the panicles and culms caused by inclement weather conditions which set in before harvesting was effected.

The parent lines, also allowed to grow to maturity, were similarly damaged by wind and rain, but after eliminating the damaged individuals a number of plants remained on which culm and spikelet determinations were obtained. The data relating to these and to the family 709 Cn are summarised in Table II.

The records relating to the parental lines and to the F_2 plants of 709 Cn are perhaps not strictly comparable on account of the different stages of maturity at which the respective determinations were made. Slight differences in average length of culms may be present, but the number of spikelets, and possibly the number of culms too, should show little or no disparity on this account.

The inheritance of number of spikelets.

The parent lines. From Table II it will be seen that the marked difference in spikelet numbers obtained between the L_1 plants of the fatuoid and normal parents is reproduced in the plants of the L_2 generation. Whether the unit of study employed is the plant, the culm or the main culm per plant, the average number of spikelets in the fatuoid offspring show average figures significantly lower than those of the normal.

In all three comparisons it will be seen that the fatuoid plants produce little more than half the number of spikelets borne by plants of the normal or type strain, and that this difference in spikelet number is in each case statistically significant.

The F_2 *generation.* From Table II it is clear that in the F_2 family 709 Cn the inheritance of spikelet number is very closely associated with

[1] In the ripe grain the normals are fairly readily distinguished from the intermediates by their distinctly yellow colour of grain, but in the immature plants division solely on the basis of awn development and basal hairs failed to give satisfaction.

[2] That is, the heterozygous fatuoid and homozygous normal phenotypes grouped together.

TABLE II.

Showing data relating to culm and spikelet analysis in the parent lines and F_2 *segregates of the cross Golden Rain fatuoid × normal*—1927.

Phenotypes	General Data: No. of seeds sown	No. germinated	Damaged plants	No. investigated	Average per plant: No. of culms	Length of culms in cm.*	No. of spikelets	Average per culm: No. of spikelets	Average per main culm per plant: No. of spikelets	Length of main culm in cm.
rent lines:										
Golden Rain fatuoid Cn 578/2	50	50	19	31	3·19 ± 0·10	113·16 ± 1·58	62·9 ± 3·17	19·22 ± 0·53	23·7 ± 0·56	124·5 ± 1·80
Golden Rain normal Cn 577/2	50	49	21	28	3·32 ± 0·11	117·17 ± 1·38	121·9 ± 5·06	37·21 ± 1·36	49·46 ± 2·24	130·3 ± 1·40
Mean difference†	—	—	—	—	*+0·13 ± 0·14*	*+4·01 ± 2·09*	**+59·0 ± 5·97**	**+17·99 ± 1·46**	**+25·76 ± 2·53**	*+5·8 ± 2·28*
segregates: *ex* 709 Cn	100	99	4							
Homozygous fatuoid				29	2·72 ± 0·13	119·27 ± 1·56	62·0 ± 3·65	21·9 ± 0·69	26·60 ± 0·91	127·9 ± 1·66
Mean deviation†				—	*−0·47 ± 0·16*	—	*−0·9 ± 4·83*	*+2·68 ± 0·87*	*+2·90 ± 1·07*	—
Heterozygous fatuoid and homozygous normal				66	3·09 ± 0·09	118·68 ± 1·04	90·1 ± 3·36	29·1 ± 0·60	35·33 ± 0·72	127·4 ± 1·12
Mean deviation†	—	—	—	—	*−0·10 ± 0·13*	—	**+27·2 ± 4·61**	**+9·88 ± 0·80**	**+11·63 ± 0·91**	—

* Measurements taken from the base of the culm to the apex of the panicle.
† Mean deviation plus or minus when compared with Cn 578/2, the fatuoid parent line.

type of grain, the average number of spikelets in the homozygous fatuoid class being practically identical with that of the fatuoid parent line. Though there are small differences in average numbers per culm and per main culm, these are of doubtful significance.

On comparing the figures for the average number of spikelets per plant in the fatuoid segregates with those of the non-fatuoid class, a very marked difference is evident. The non-fatuoids average $90{\cdot}1 \pm 3{\cdot}36$ as against $62{\cdot}0 \pm 3{\cdot}65$, the average of the fatuoid class. The mean difference of $28{\cdot}1 \pm 4{\cdot}96$, however, is distinctly less than that which occurs between the fatuoid and the normal parent lines, namely, than $59{\cdot}0 \pm 5{\cdot}97$. The grouping of the heterozygous fatuoids and the normals into one class as "non-fatuoids" possibly accounts in part for this narrowing of the average difference, but not completely as will be seen from the F_3 studies discussed below (cf. p. 24).

Similar comparisons between the fatuoids and the non-fatuoid segregates on a culm or main culm basis also show the same narrowing of the average differences in spikelet numbers, the figures *per culm* in round numbers being 19 and 37 in the fatuoid and normal lines respectively, and 22 and 29 in the fatuoid and non-fatuoid segregates; and per *main culm* 24 and 49 as against 27 and 35 respectively.

This general narrowing of the average difference is brought out more clearly when the average length per main culm is divided by the average number of spikelets per main culm, namely, by the culm length spikelet number ratio. The figures so obtained are—fatuoid line, 5·2; normal line, 2·6; fatuoid segregates, 4·8; non-fatuoid segregates, 3·6. There is thus not only a lowering of the average number of spikelets in the non-fatuoids (due partly to the inclusion of the heterozygous fatuoids), but also a slight increase in average spikelet number in the fatuoid segregate class.

Culm inheritance. In making a comparison of the average number of culms per plant in the parent lines, no evidence is to be found of any significant differences in the behaviour of this character. The fatuoid has an average number of culms of $3{\cdot}19 \pm 0{\cdot}10$ and the normal $3{\cdot}32 \pm 0{\cdot}11$, and the mean difference of $0{\cdot}13 \pm 0{\cdot}14$ is less than the probable error of the difference.

In the segregate classes the averages for the fatuoids and non-fatuoids are $2{\cdot}72 \pm 0{\cdot}13$ and $3{\cdot}09 \pm 0{\cdot}09$ respectively, and the mean difference $0{\cdot}37 \pm 0{\cdot}21$. The fatuoid average is somewhat low, but in comparison with the non-fatuoid class its deviation is not significant.

In both line and segregate material there is, however, a tendency for

the fatuoid individuals to be slightly lower than the normals, but in neither case do the deviations appear to be significant.

Length of culm. In average length of culm per plant, the parent lines agree fairly closely; the fatuoids on the average are very slightly shorter, but the mean difference of $4 \cdot 01 \pm 2 \cdot 09$ is not significant. The average length of the fatuoid is seen from Table II to be $113 \cdot 16 \pm 1 \cdot 58$ cm. and of the normals $117 \cdot 17 \pm 1 \cdot 38$ cm.

The averages per main culm are $124 \cdot 5 \pm 1 \cdot 80$ and $130 \cdot 3 \pm 1 \cdot 40$, but the difference on this basis of $5 \cdot 8 \pm 2 \cdot 28$ is not of any statistical significance.

The segregate groups, however, show closer agreement with one another than do the lines both on the *per plant* and *per main culm* basis; the figures per plant being $119 \cdot 27 \pm 1 \cdot 56$ and $118 \cdot 68 \pm 1 \cdot 04$ cm. for fatuoid and non-fatuoid groups; and per main culm $127 \cdot 9 \pm 1 \cdot 66$ and $127 \cdot 4 \pm 1 \cdot 12$ cm. respectively. The similarity between the two classes in both comparisons is here remarkably close.

The F_3 *and* L_3 *generations.*

The F_3 data are confined to the inheritance of spikelet number in relation to fatuoid, intermediate and normal types of grain. Counts were made of the numbers of spikelets on the main culms of single spaced plants in 42 F_3 families and in the L_3 plants of the respective parent strains. The spikelet averages for the several families are shown in Table III. For convenience of analysis the individual F_3 families are arranged in their respective genetical groups.

The parental lines. In this material the average difference in spikelet number between the two parental lines, Cn 578/3 and Cn 577/3 respectively, is of much the same order as what was found to occur in the L_2 generations (cf. Table VI). Since spikelet number varies with soil fertility, complete agreement in the actual average numbers of spikelets between the L_2 and L_3 plants is not to be expected; the average differences nevertheless are remarkably close.

The segregate families. In growing the F_3 material, the individual families were arranged in single-traverse beds in serial sequence, *i.e.* starting with family 713 Cn 1 and following with 713 Cn 2, etc., up to 713 Cn 50, and not in the order given in Table III. Owing to the absence of any replication of the different beds, direct comparisons between individual families unfortunately cannot be made on account of possible errors arising through soil variation. But if comparisons are made between the average of the homozygous fatuoid families as a whole, and the average of the homozygous normal also as a whole, the soil effects are

neutralised by the random distribution of the several family beds. In the segregating families the random distribution of the segregates in each bed permits of direct comparisons being made between the respective averages of the fatuoid, intermediate and normal phenotypes within each segregating family, as well as between the totals of the fatuoids, intermediates and normals of all the segregating families.

Table III shows that there is still a very decided association between low spikelet number and fatuoid type of grain, the figures for F_3 fully confirming those for F_2.

Table III also shows that the average spikelet number in the heterozygous classes of the segregating F_3 families is practically intermediate between those of the fatuoid and normal classes. The effect of grouping the heterozygous fatuoid and normal plants, as carried out in the F_2 material (Table II), is to cause a narrowing of the difference between the fatuoid and non-fatuoid averages. But the F_3 data also show that the tendency to convergence between the average figures for the fatuoid and non-fatuoid groups as shown in Table II is not completely explained as an effect of grouping the heterozygotes and normals; for it will be seen that a slightly lower average number of spikelets occurs in the normal segregate class as compared with the normal line (Cn 577/3), as well as a slight upward shift in the fatuoid segregate class as compared with the fatuoid line (Cn 578/3).

A conceivable explanation of this change in the general average values of the segregates, as compared with the parent lines, is that some degree of crossing-over between the respective factors for low spikelet number and fatuoid type of grain on the one hand, and high spikelet number and normal grain on the other, may be taking place. If so, the F_3 generation should give (1) families homozygous for fatuoid grain and high spikelet numbers, (2) families homozygous for normal grain with low spikelet number, and (3) families segregating into fatuoids with high and normals with low spikelet numbers.

But for the unknown effect of the soil factor, family 713 Cn 23, with an average of 43·0, might be singled out as an example of a homozygous fatuoid family with high spikelet number, and families 713 Cn 44 and 48, with averages of 33·0 and 34·0, respectively, as instances of homozygous normals with low spikelet number; but in the absence of replication, as explained above, no values can be given as to the significance of these figures for individual family comparisons.

Further, among the F_3 segregating families, 713 Cn 31, 713 Cn 34 and 713 Cn 42 show remarkably close agreement between the averages for

TABLE III.

Showing spikelet inheritance in relation to the phenotypes homozygous fatuoid, heterozygous fatuoid and homozygous normal in F_3 *families of the cross Golden Rain normal × fatuoid*—1927.

F_2 classification and reference numerals	No. of seeds sown	Breeding behaviour in F_3 generation: Homozygous fatuoid	Breeding behaviour in F_3 generation: Heterozygous fatuoid	Breeding behaviour in F_3 generation: Normal homozygous	Ratio of fatuoid : non-fatuoid	Average spikelet distribution per main panicle in F_3 phenotypes: Homozygous fatuoid	Average spikelet distribution per main panicle in F_3 phenotypes: Heterozygous fatuoid	Average spikelet distribution per main panicle in F_3 phenotypes: Normal	No. of plants examined
Parent lines:									
Golden Rain fatuoid Cn 578/3	50	All	—	—	—	27·3 ±0·64	—	—	40
Normal, Cn 577/3	50	—	—	All	—	—	—	51·6 ±1·61	40
Mean difference	—	—	—	—	—		24·3 ±1·73		—
Segregate families:									
Homozygous fatuoid									
713 Cn 1	50	All	—	—	—	35·2	—	—	38
4	50	,,	—	—	—	29·8	—	—	46
5	50	,,	—	—	—	35·5	—	—	40
9	10	,,	—	—	—	35·4	—	—	7
11	50	,,	—	—	—	26·6	—	—	46
13	50	,,	—	—	—	30·7	—	—	44
14	50	,,	—	—	—	35·5	—	—	44
15	50	,,	—	—	—	34·6	—	—	41
16	50	,,	—	—	—	35·0	—	—	47
18	10	,,	—	—	—	35·0	—	—	7
23	20	,,	—	—	—	43·0	—	—	16
25	20	,,	—	—	—	37·1	—	—	19
35	50	,,	—	—	—	26·7	—	—	39
37	50	,,	—	—	—	24·5	—	—	44
40	50	,,	—	—	—	27·4	—	—	43
45	20	,,	—	—	—	31·4	—	—	18
Total or average	630	539	—	—	—	32·7 ±0·78	—	—	539

Heterozygous fatuoid									
713 Cn 7	50	5	25	14	1 : 7·8	32·4	42·2	38·8	44
10	50	7	23	8	1 : 4·4	33·8	41·5	53·6	38
17	50	8	26	8	1 : 4·3	28·4	33·8	52·4	43
20	50	12	22	8	1 : 2·5	36·5	42·3	42·9	42
22	50	14	18	9	1 : 2·0	30·4	37·2	50·5	41
26	50	7	23	8	1 : 4·4	37·0	45·3	45·2	38
27	50	9	31	7	1 : 4·2	30·0	38·2	40·0	47
29	50	10	25	11	1 : 3·6	32·0	34·8	48·3	46
30	50	9	20	10	1 : 3·3	24·0	25·0	30·5	39
31	50	9	20	6	1 : 2·9	31·2	39·6	32·8	35
32	50	14	23	8	1 : 2·2	28·7	34·1	32·6	45
34	50	12	18	12	1 : 2·5	33·2	38·1	32·0	42
36	50	8	28	12	1 : 5·0	21·4	26·4	29·0	48
38	50	9	17	13	1 : 4·7	26·9	32·5	36·4	39
39	50	16	21	6	1 : 1·7	32·0	32·0	47·5	43
41	50	10	18	10	1 : 2·8	37·1	41·5	43·1	38
42	50	8	25	11	1 : 4·5	26·0	31·0	26·6	44
46	50	17	25	7	1 : 1·9	25·2	29·[illegible]	45·1	49
Total or average	900	184	408	168	1 : 3·13	30·3 ±0·68	35·8 ±0·88	40·4 ±1·14	761
Calculated (1 : 2 : 1)	—	190·25	380·50	190·25	—	—	—	—	—
Homozygous normal									
713 Cn 2	50	—	—	All	—	—	—	51·9	40
8	50	—	—	,,	—	—	—	48·0	46
21	50	—	—	,,	—	—	—	39·2	43
33	50	—	—	,,	—	—	—	39·2	40
44	50	—	—	,,	—	—	—	33·0	44
47	50	—	—	,,	—	—	—	53·4	44
48	50	—	—	,,	—	—	—	34·0	45
50	20	—	—	,,	—	—	—	42·0	18
Total or average	370	—	—	320	—	—	—	42·6 ±1·72	320

the fatuoid and the normal classes. The respective figures for the three families in the order named are 31·2 and 32·8, 33·2 and 32·0, and 26·0 and 26·6 for fatuoids and normals respectively; but the occurrence of averages of 39·6, 38·1 and 31·0 respectively for the intermediate classes do not, however, conform well unless of course we attribute their higher average values to heterosis.

Fairly high average figures in all three genotypes are seen in the family 713 Cn 41, namely, 37·1, 41·5 and 43·1 respectively, but the fatuoid class remains lower than the normal, whilst the heterozygous class is more or less intermediate. The fatuoid figure, however, is distinctly high in this family, and the difference between it and the normal is not so very considerable.

No examples, however, are to be found within the segregating families of fatuoids with high and normals with low spikelet numbers, but in a study of only eighteen families, especially should the percentage of cross-overs be low, this may possibly be due to the absence of completely representative F_3 cultures.

In general, therefore, the F_3 data show that the fatuoid of Golden Rain differs markedly from the type variety in average number of spikelets, which difference is associated in inheritance with the fatuoid kind of grain. The slight narrowing of the average difference in spikelet number between the fatuoid and normal segregates is seen to be due partly to a slight increase in the average of the fatuoid segregates, and partly to a somewhat similar and corresponding decrease in the average of the normal segregates. This narrowing effect is such as might occur as the result of crossing-over between the factor or factors for low spikelet number and fatuoid type of grain on the one hand, and for high spikelet number and normal type grain on the other.

(*b*) Fulghum fatuoid × Fulghum normal.

Reciprocal crosses were made between representative plants of fatuoid and normal Fulghum in the summer of 1924, and four hybrid seeds, namely 910–913 Cn, were produced. These crosses were originally made with a view to the study of segregation of the grain characters "fatuoid" and "normal," but when the association between fatuoid grain and spikelet number in the Golden Rain material was observed, it was decided to extend the scope of the investigation to cover panicle exsertion and spikelet and culm distributions.

In so far as external characters are concerned, the Fulghum fatuoid appears to belong to the *A* series group (see Plate II, fig. 21 (*a*) *left*).

The F_1 *and* L_1 *generations.*

F_1 hybrids and L_1 parent progenies of this cross show complete similarity in the early and late stages of vegetative growth, both in the degree of pubescence of leaf-sheath and leaf-margin, and in their general appearance and habit of growth. With regard to the date of panicle emergence and height-to-ligule of the uppermost leaf at this date, very close agreement exists between the hybrids and the line generation plants, and this is also true for counts of the number of panicle-bearing culms.

In grain characteristics such as type of base, pubescence, and awn development, the F_1 hybrids show close resemblance to the normal parent line, from which they differ only in the slightly less solidified base, in the basal hairs being rather more frequent, and in the occurrence of a few hairs on the rachilla in some of the spikelets. The awns on the lower grains, however, occur rather more frequently than in the normal strain, and like those of the latter are weak, medium-long and not, or only very rarely, twisted at the base. The upper grains are awnless and the florets disjoin as in the normal parent strain, *i.e.* in a typical *A. sterilis* manner. The character of the awn in the F_1 of this cross is, however, different from that occurring in the F_1's of crosses between fatuoids and normals of the *A. sativa* species. In the latter the awn is definitely twisted, and generally strong, and appears on most, if not on all, of the lower grains, whereas in the Fulghum hybrid it is weak, generally non-twisted and rather variable in the frequency of its occurrence. These latter features make separation of the intermediate and normal phenotypes a matter of considerable difficulty in the progeny of this cross.

The F_2 *and* L_2 *generations*—1926.

Owing to lack of adequate cage space only small F_2 families could be grown in 1926. These were raised from seed of the F_1 plants 910 and 911 Cn. From each, 50 grains were sown in "paired-drills," and 10 grains of each of the parent lines were sown alongside for comparison. Owing to unfavourable growing conditions during the early part of the 1926 season, vegetative development was decidedly poor, the plants produced were small, and a few died off before panicles were exserted. Counts were made of the number of spikelets on the main panicle of each plant when the heads were fully emerged, and at the same time the category of the segregate, that is, whether fatuoid or non-fatuoid, was recorded[1]. These data are shown in Table IV.

[1] An attempt was made to classify the segregates into fatuoid, intermediate and normal, but this had to be abandoned owing to the difficulty of accurately distinguishing the plants of intermediate and normal phenotypes.

TABLE IV.

Showing spikelet distribution in relation to type of grain in the F_2 *generation of reciprocal crosses between Fulghum fatuoid × normal*—1926.

Description of cross or parents	Parent or hybrid reference	No. of seeds sown	No. of plants available for study 2/7/26*	Type of grain: Homozygous fatuoid	Type of grain: Heterozygous fatuoid or normal	Average no. of spikelets per main culm: Fatuoid	Average no. of spikelets per main culm: Non-fatuoid
Fulghum fatuoid × normal	910 Cn	50	43	14	29	7·7 ±0·48	8·3 ±0·31
Reciprocal	911 Cn	50	42	10	32	8·2 ±0·42	7·03 ±0·21
Totals or averages	—	100	85	24	61	7·91 ±0·33	7·65 ±0·19
Mean difference	—	—	—	—	—	0·26 ±0·38	
Expected segregates on 1 : 3 basis	—	—	—	21·25	63·75	—	
Parent lines:							
Fulghum fatuoid	Cn 738/2	10	8	All	—	8·13 ±0·58	—
Fulghum normal	Cn 739/2	10	10	—	All	—	9·10 ±0·42
Mean difference	—	—	—	—	—	0·97 ±0·72	

* No record was made of the number of seeds which germinated.

Segregation for type of grain (columns 5 and 6) is evidently unifactorial.

The average spikelet number in the fatuoids and the non-fatuoids is very close, and there is no evidence of any association of low spikelet number with fatuoid type of grain either in the fatuoid line or in the extracted fatuoid segregates.

The F_2 *and* L_2 *generations*—1927.

In 1927 a more extended study was carried out with seed from the same source as that used in 1926, but instead of sowing the grain *in situ* all lots were sown in boxes and placed in a cool greenhouse to germinate, the seedlings being later planted out into a bird-proof cage.

Comparison of dates of panicle exsertion. During the growing season records were made of the date of commencement of panicle exsertion in both parental and hybrid material, these data being taken on alternate days so far as was possible. The figures so obtained are shown in Table V. In general, the agreement between the F_2 populations and the two parental lines is quite good. It is true that a minor peak occurs in the period 28 June to 13 July, but this occurs in both hybrid and parent strains alike, and is largely due to delay in panicle exsertion following upon injury through frit fly and other plant pests. The actual distribution is therefore better expressed by the 11-day period, 13–24 June, within which the hybrid families show a very definite uni-modal arrangement and give no indication of any factorial segregation taking place. The segregates in general, however, appear from the data to be a little earlier exserting than the parent lines.

The index of panicle exsertion employed in this study was the date when the apical spikelet of the first shoot to exsert was fully emerged. According to Florell (7) the date of emergence of the tip of the first spike is considered to be the most dependable index for studying earliness in cereals. This being so, the distribution shown in Table V may also be regarded as the frequency distribution in respect of earliness. It is clear that for earliness and date of panicle emergence there are no marked genetical differences between the parent strains and segregates.

Segregation for type of grain. A summarised analysis of the F_2 segregation for type of grain in relation to culm and spikelet inheritance is given in Table VI. Figures are also given in this table for culm and spikelet characters in the respective parental lines. From 200 seeds sown, and a percentage germination of 99, 194 F_2 plants survived to maturity. Of these 48 were fatuoid and 146 non-fatuoid, a clear mono-hybrid

TABLE V.

Frequency distribution of dates of commencement of panicle exsertion of F_2 *generation segregates and parent lines of Fulghum fatuoid × normal and reciprocal*—1927.

Description of hybrids and parents	Reference to hybrid and parent	No. of seeds sown	No. germinated	No. planted out	Dates of commencement of panicle exsertion: 13/6	15/6	17/6	20/6	22/6	24/6	26/6	28/6	1/7	4/7	8/7	13/7	Total
Hybrids:																	
Fulghum fatuoid × normal	910 Cn	100	98	98	20*	29	35	6	1	2	—	—	1	—	3	—	97
Reciprocal	911 Cn	100	100	100	7	25	42	5	3	2	—	3	4	4	4	1	100
F_2 segregate total	—	—	—	—	27	54	77	11	4	4	—	3	5	4	7	1	197
Parent lines:																	
Fulghum fatuoid	Cn 738/2	10	10	10	—	1	2	2	1	1	—	1	2	—	—	—	10
Fulghum normal	Cn 739/2	10	10	10	—	—	2	6	1	—	—	—	—	—	1	—	10

* Includes a number of plants which exserted a few days earlier than 13/6.

TABLE VI.

Showing segregation in the F_2 *generation of Fulghum fatuoid × normal and reciprocal for type of grain, average number of culms and average number of spikelets on main culm; also data on parent lines*—1927.

Description of hybrids and parents	Reference to hybrids and parents	No. of seeds sown	Germination %	F_2 segregation for type of grain: Fatuoid	Non-fatuoid	Average no. of culms per plant*: Fatuoid	Non-fatuoid	Average no. of spikelets per main culm*: Fatuoid	Non-fatuoid
Fulghum fatuoid × normal	910 Cn	100	98	25	70	6·22 ± 0·17	6·09 ± 0·14	10·45 ± 0·45	10·68 ± 0·28
Reciprocal	911 Cn	100	100	23	76	6·70 ± 0·28	5·91 ± 0·15	10·20 ± 0·40	9·92 ± 0·28
Totals or average	—	200	99	48	146	6·45 ± 0·16	6·00 ± 0·15	10·33 ± 0·21	10·30 ± 0·19
Mean difference	—	—	—	—	—	0·45 ± 0·22		0·03 ± 0·28	
Expected (1 : 3)	—	—	—	**48·5**	**145·5**				
Parent lines:									
Fulghum fatuoid	Cn 738/2	10	100	10	—	8·0 ± 0·31	—	11·3 ± 0·53	—
Fulghum normal	Cn 739/2	10	100	—	10	—	7·7 ± 0·43	—	15·6 ± 0·75
Mean difference	—	—	—	—	—	0·30 ± 0·53		4·3 ± 0·92	

* Owing to the occurrence of damaged culms and panicles these determinations were made on only 22 fatuoid and 66 non-fatuoid plants in 910 Cn and 20 fatuoids and 66 non-fatuoids in 911 Cn.

segregation. Evidently the characteristic distinguishing features of the fatuoid and the normal grain in this cross behave genetically as single contrasting units, and in this respect show complete conformity with fatuoid × normal crosses of the species *A. sativa*.

These data, however, differ from those obtained by Stanton, Coffman and Wiebe (20), who obtained a complex segregation in a study of similar varietal material. They consider that the fatuoids of Fulghum and Burt, both varieties of *A. sterilis culta*, are genetically different from those found in *A. sativa* varieties, and probably differ from the normal by several factors. They also found that the fully developed fatuoid grain did not invariably breed true.

Throughout the present study the parental lines of both the fatuoid and the normal strains have continued in all cases to breed true.

Culm inheritance. From columns 7 and 8 of Table VI it will be seen that in average number of culms per plant the fatuoid and non-fatuoid segregates show no important deviations from one another. The figures for the parent lines are slightly higher, but this is probably due to differences in soil fertility, since the parent lines were grown in separate beds adjoining, but not interspaced with, the segregate material. The parent lines, however, agree closely amongst themselves in average culm production.

Spikelet inheritance. In the last two columns in Table VI, the average number of spikelets per main culm in the fatuoid group of the combined families 910 and 911 Cn is seen to be $10{\cdot}33 \pm 0{\cdot}21$, and in the non-fatuoid group $10{\cdot}30 \pm 0{\cdot}19$, a very close agreement. The parental lines, on the other hand, differ rather widely—$11{\cdot}3 \pm 0{\cdot}53$ and $15{\cdot}6 \pm 0{\cdot}75$, fatuoid and normal respectively—the mean difference being $4{\cdot}3 \pm 0{\cdot}92$, which is more than four times the probable error of the difference. The general average is also higher as compared with the averages of the fatuoid and non-fatuoid segregates, but this may be connected with soil inequalities as explained in connection with culm inheritance above.

In the parent strains grown in 1926 the observed averages showed no differences of statistical significance, but the small average difference which did occur was in the same direction as that obtained in the 1927 material, namely, towards a slightly higher average number in the normal line. The occurrence and significance of this slight increase in favour of the normal line is being further investigated with larger numbers of plants.

In general we may conclude that the data on the Fulghum fatuoid × normal cross demonstrate no genetical differences between fatuoid and

normal plants in respect of date of panicle emergence, and that with regard to culm and spikelet characters complete genetical similarity exists. There is in the segregate material of this cross no association of low spikelet number with fatuoid type of grain, such as occurs in the Golden Rain fatuoid × normal cross described above.

(c) Fulghum fatuoid (*A. sterilis culta*) × Grey Winter normal (*A. sativa*).

The reciprocal crosses between Fulghum fatuoid and Grey Winter normal were made in 1925. The grain of the latter variety has been described by Marquand (17) as possessing awns few in number, twisted and geniculate, the lower grain frequently bearing a small tuft of hairs at its base.

The cross Fulghum fatuoid × Grey Winter normal gave seven hybrid seeds (997–1003 Cn) and the reciprocal two seeds (1004 and 1005 Cn).

The F_1 *generation.*

Sown in the spring of 1926, all nine seeds germinated and produced plants which appeared to be definitely hybrid in character, and no differences were apparent between the individuals of the reciprocal pollinations. The F_1 hybrids, however, differed from those of the Fulghum fatuoid × normal cross, described above, by the occurrence of fairly strong, twisted and sub-geniculate or geniculate awns on all the lower grains. In this respect they agree closely with the F_1 hybrids which occur when both the normal and fatuoid parents belong to the *A. sativa* species.

The F_2 *and* L_2 *generations.*

F_2 families were grown in 1927 from seed of the reciprocal hybrids 1000 Cn and 1005 Cn. Of each hybrid 100 and of each parent line 10 seeds were sown in boxes and germinated well in a cool greenhouse.

In Table VII, columns 5, 6 and 7, is shown the segregation for fatuoid, intermediate and normal type of grain. Unlike the Fulghum fatuoid × normal cross, the intermediate and the normal phenotypes are here fairly readily distinguished, and there is obvious segregation on a 1 : 2 : 1 basis.

One plant of doubtful relationship appeared in the family 1005 Cn and has been included in the intermediate class. It possessed spikelets of intermediate character in respect of pubescence and basal articulation, but both grains of the spikelets possessed weak awns.

The two parental lines continued throughout to breed true for their respective types of grain.

TABLE VII.

Showing F_2 *segregation for type of grain in reciprocal crosses of Fulghum fatuoid × Grey Winter normal; also the breeding behaviour of the parent lines*—1927.

Description of hybrids and parents	Reference numerals	No. of seeds sown	No. germinated	Phenotypical classification of F_2 segregates for type of grain: Fatuoid	Intermediate	Normal	Unclassed	Totals including damaged plants
Fulghum fatuoid × Grey Winter normal	1005 Cn	100	99	16	45*	22	16	99
Reciprocal	1000 Cn	100	98	27	45	19	7	98
Totals	—	200	197	43	90	41	23	197
Expected (1 : 2 : 1)	—	—	—	43·5	87	43·5	—	—
Total fatuoid : non-fatuoid	—	—	—	43	131		—	—
Expected (1 : 3)	—	—	—	43·5	130·5		—	—
Parent lines:								
Fulghum fatuoid	Cn 917/2	10	10	10	—	—	—	10
Grey Winter normal	Cn 916/2	10	10	—	—	10	—	10

* Includes one plant of the "weakly awned" type.

(*d*) FULGHUM FATUOID × GOLDEN RAIN FATUOID.

In order to test further the genetical similarity or otherwise of the factor, or factor-group, which determines the fatuoid character in *A. sterilis culta* var. Fulghum, with that which gives rise to the fatuoid character in varieties of *A. sativa*, a fatuoid of Fulghum was hybridised with a fatuoid of the variety Golden Rain. From hybridisations carried out in 1925 five hybrid seeds were produced, viz. 1008–1012 Cn.

The F_1 *generations.*

All five F_1 plants (1008–1012 Cn) were grown in 1926, and all produced homozygous fatuoid type of grain. Apart from 1012 Cn, which was a small plant, all were much alike in height of plant and culm-producing capacity. All five, however, possessed many florets which failed to produce caryopses, though the paleae were normally developed. In consequence of the freely disarticulating fatuoid base, much of the grain was shed before the plants were fully matured, and the actual percentage of failures was not determinable; but from the grains still adhering when the plants were examined after harvesting, counts were made of the number of fertile and empty grains then present. The numbers of spikelets borne by each plant were also determined for all except 1008 Cn. As shown in Table VIII, approximately one-third of the grains were

TABLE VIII.

Showing number of spikelets and number of fertile and empty grains (when harvested) in five F_1 *plants of the cross Fulghum fatuoid × Golden Rain fatuoid*—1926.

Hybrid designation	Total no. of spikelets per plant	No. of fertile grains	No. of empty grains
1008 Cn	—	94	43
1009 Cn	164	108	51
1010 Cn	111	74	48
1011 Cn	189	136	49
1012 Cn	60	5	21
Totals	524	417	212

empty. Assuming an average of two grains per spikelet to have been originally present, an under- rather than an over-estimate, a loss of grain, through shedding, of approximately 50 per cent. has taken place. It is, of course, impossible to estimate the significance of the proportion of empty to fertile grains in the figures given, owing to the unknown ratio of fertile to empty grains in the shattered seed. One would expect,

however, that on account of their heavier weight, more fertile grains than empty ones would have fallen; in which event the actual proportion of empty to fertile would be greatly reduced. But whatever the number of empty grains in the shed seed, the numbers actually occurring on the several F_1 plants when harvested are exceptionally high.

The F_2 *and* L_2 *generations.*

F_2 generations from 1009 Cn and 1011 Cn were grown in 1927. Of the former 97 and of the latter 100 seeds, together with 10 seeds of each parent strain, were germinated in boxes in the usual manner, and all produced mature plants of normal size and vigour. When harvested the segregates and parents were examined for the presence or absence of normal or intermediate types of grain, and the results are shown in Table IX.

TABLE IX.

Showing data on the F_2 *generation and parent lines of the cross Fulghum fatuoid × Golden Rain fatuoid*—1926.

Description of hybrids and parents	Reference numerals	No. of seeds sown	No. germinated	Phenotypical classification of type of grain: Fatuoid	"Intermediate"	Normal
Fulghum fatuoid × Golden Rain fatuoid	1009 Cn	97	96	90	2	—
Reciprocal	1011 Cn	100	95	75	3	—
Totals	—	197	191	165	5	—
Parent lines:						
Fulghum fatuoid	Cn 957/2	10	9	9	—	—
” ”	Cn 965/2	10	10	10	—	—
Golden Rain fatuoid	Cn 964/2	10	10	10	—	—

The three parental lines Cn 957/2, Cn 965/2 and Cn 964/2 respectively yielded plants all bearing homozygous fatuoid type of grain. The lines and segregates all showed complete survival when the plots were examined about the time of the commencement of panicle emergence, but during the course of harvesting and subsequent handling, several plants were damaged, and when the lots were investigated in the laboratory only 170 individuals out of a possible 191 in the two F_2 families were separable as single and complete plants. Of the broken and detached panicles none showed deviation from the homozygous fatuoid type of grain. The 170 undamaged F_2 plants consisted of 165 homozygous for fatuoid type of grain and five which were non-fatuoid; the spikelets of the latter were of an intermediate or heterozygous fatuoid character.

These five non-fatuoid plants are shown in column 6 of Table IX under the heading "intermediate." The spikelets borne by these individuals represented outwardly the heterozygous fatuoid phenotype; the lower grains possessed fairly strong, twisted and slightly geniculate awns and a slightly pubescent and partially solidified base, while the upper grains were awnless[1].

Probably these five plants originated through natural crossing in the F_1 generation by stray pollen of normal genotype. That natural crossing does occasionally occur in the F_1 has been shown in connection with the appearance of black-grained heterozygous fatuoid plants in artificial crosses between non-black and non-fatuoid parents (see pp. 8–9). The F_1 were not artificially protected against the possibility of fertilisation by foreign pollen, and for this reason further investigations with F_2's from assured selfed F_1 plants appear to be necessary in order to establish with certainty the origin of such individuals. The occurrence of "intermediates" under such conditions would annul the theory of their origin by natural crossing.

The result of inter-crossing the fatuoids of Fulghum and Golden Rain, apart from the five "intermediates," indicates a similarity of genotype in respect of the fatuoid characters in these two specific strains. It is the writer's belief that the F_1's of this cross, when protected against all possibility of fertilisation by foreign pollen, would give only homozygous fatuoid offspring.

(*e*) Scotch Potato normal (*A. sativa*) × *A. nuda* fatuoid.

As explained in an earlier section of this paper (p. 7) the *A. nuda* plant used as parent in the cross Scotch Potato × *A. nuda* was found to be heterozygous for the fatuoid character, and two of the artificial hybrids, viz. 629 and 630 Cn, were found to be hybrid in this respect.

The F_2 generation raised from family 629 Cn gave 21 fatuoid and 70 non-fatuoid plants from 100 seeds sown, and from a like number, family 630 Cn gave 19 fatuoid and 70 non-fatuoid segregates. The totals for both families are 40 fatuoid and 140 non-fatuoid, where expectation is 45 and 135. There is a slight deficiency in the homozygous fatuoid class, but it was not always easy in this material to detect the homozygous fatuoid genotypes when present in the homozygous *nuda* type of spikelets, and this may account at least for some of the disparity in respect of this class.

[1] In 1929 the progenies of each of these plants showed segregation into fatuoids, intermediates and normals.

In the segregates with *nuda* type of spikelets, only those possessing strong awns on all the paleae were included in the fatuoid class.

In a few selected F_3 families of this cross a new "awned" type of grain was seen to occur in certain of the hulled families. The spikelets of this new type closely resemble those of heterozygous fatuoid plants in outward grain characters. The lower grain has a very strong, twisted and geniculate awn which, however, is distinctly stronger than that of the typical *A* series heterozygous fatuoid, and is closely similar to a fully developed fatuoid awn; basal pubescence occurs as small lateral tufts; and the upper grain is awnless. Some of the families contained both normal and "awned" plants, while other families consisted entirely of plants of the "awned" type. The latter families were apparently homozygous for the new character. This new form is morphologically very similar to Type C, described above (see p. 16), which occurred as a segregate in the F_2 generation of the cross Red Rustproof × Scotch Potato. Since the variety Scotch Potato is a parent common to both crosses, the occurrence of somewhat similar "awned" types in the segregating progeny of these two crosses may possibly be related to the particular genetical constitution of this variety. But further observation and study are necessary before this point can be made clear.

(*f*) Strongly awned Type A (*ex* Ceirch-du-bach) × Supreme (*A. sativa*) fatuoid.

Four F_1 hybrid plants (904–907 Cn) were grown in 1925 from reciprocal crosses between the strongly awned Type A strain of Ceirch-du-bach and a fatuoid of the cultivated variety Supreme. The Type A plant was the seed parent of 904 Cn and the pollen parent of 905–907 Cn. The object of the cross was to study the inter-relationships of Type A and fatuoid grain characters.

The parent strains are alike in being black, in possessing strong, twisted and geniculate awns on the first and second grains, and in exhibiting a tendency to shed when ripe. But the fatuoid has a horseshoe-shaped basal articulation in all grains of the spikelet, an almost complete ring of dense, short pubescence (about 1 mm. or less) on the basal callus, and dense pubescence on the rachilla; while Type A has an oval-shaped cavity at the base of the lower grain, and the base of the upper is completely solidified. Pubescence in Type A is confined to the occurrence of dense lateral tufts about 2–4 mm. long at the base of the lower grain, and to slight hairiness of the rachilla, the upper grain being completely glabrous (see figs. 13 and 14, Plate I).

The F_1 generation.

F_1 plants of the reciprocal crosses were all alike phenotypically. In respect of the contrasting grain characters, they showed close similarity to the Type A parent, differing only in the very slightly enlarged and slightly less solidified articulation of the lower grain of the spikelet, and in the basal pubescence being shorter (approximately 1·0–1·5 mm. long). The upper grain of the F_1 spikelet was identical with that of the Type A strain. Apart from the reduced length of the pubescence, there appeared to be an almost complete dominance of the Type A grain characters.

The F_2 generation.

Small F_2 generations were grown from 904 and 905 Cn in 1926. On harvesting it was found that only four clearly defined classes of grain were present, namely:

(1) Type A grain with short, or fairly short, pubescence.
(2) Type A grain with long pubescence.
(3) Fatuoid grain with short, or fairly short, pubescence.
(4) Fatuoid grain with long pubescence.

The data relating to the segregation of these four classes are shown in Table X, and point clearly to a case of di-hybrid segregation.

The only pairs of contrasting characters in respect of the grain features of these two strains are long *v.* short pubescence and fatuoid *v.* Type A form of grain. No segregation occurred in respect of colour of grain, awn production or "form" of pubescence[1].

The F_3 generation.

Confirmation of the di-hybrid segregation, and of the F_2 grouping as given in Table X, was obtained by growing a number of F_3 families as single spaced plants in 1927. The actual number of seeds sown in the individual families was small, owing partly to the very poor growth and small panicles produced by the F_2 plants in 1926, and partly to loss of seed by shedding before harvesting. Altogether 32 families belonging to 904 Cn were grown, and in all cases all available seed was sown. The records and analyses relating to these are brought together in Table XI, where the respective families are arranged in genetical groups according to their F_3 breeding behaviour.

[1] That is, whether the pubescence occurs in lateral tufts at the base of the grain as in Type A, or as an almost complete ring as in the fatuoid strain.

TABLE X.

Showing the segregation of length of basal pubescence in relation to non-fatuoid and fatuoid type of grain in the F_2 *of the cross strongly awned type A* × *Supreme fatuoid*—1926.

			F_2 segregation			
			Non-fatuoid		Fatuoid	
Description of the cross	Reference numerals	No. of seeds sown	Pubescence short or fairly short	Pubescence long	Pubescence short or fairly short	Pubescence long
Strongly awned Type A × Supreme fatuoid	904 Cn	50	24	7	11	4
Reciprocal	905 Cn	50	19	8	7	5
Totals	—	100	43	15	18	9
Calculated (9 : 3 : 3 : 1)	—	—	47·7	15·9	15·9	5·3
$\frac{(o-c)^2}{c}=$	—	—	0·463	0·051	0·273	2·564

$X^2 = 3{\cdot}351$; $P = 0{\cdot}346$.

The phenotypical characters of the mother plant of each particular F_3 family are given in column 2. In the same line, and in columns 4–7, the actual numbers of F_3 plants belonging to one or other of the respective grain classes are recorded. It will be observed that the F_2 grouping into the four categories of fatuoids and non-fatuoids with short, or fairly short, and long pubescence respectively, is in complete agreement with the F_3 breeding behaviour. Fatuoid type of grain and long pubescence behave as recessive characters, and F_2's of this description show no segregation in F_3. The Type A grain and short, or fairly short, pubescence, on the other hand, behave as the dominant allelomorphs, and the F_3 progenies of F_2's of this type are either homozygous for both pairs of characters, or else heterozygous for one or other or both characters. On the basis of di-hybrid segregation nine genetical classes are expected, and the groupings in Table XI of the several F_3 families show that all these have been obtained. A comparison of the observed and calculated numbers indicates fair agreement with hypothesis.

It is of interest in connection with the general fatuoid problem to note that in this cross no new combinations in respect of awn production or "form" of pubescence have occurred in any of the hybrid generations.

It is apparent from the study of this cross that the three associated characters, articulation, pubescence and awn of the Type A and the fatuoid strains respectively behave in inheritance as simple and apparently absolutely linked groups; for in so far as the present investigations go, the awn, pubescence and articulation characters, characteristic of the

Total 46 39 85

TABLE XI.

Showing the breeding behaviour of F_3 *families of the cross strongly awned Type A × Supreme fatuoid*—1927.

Reference numerals	Phenotypical classification in F_2	No. of seeds sown	Breeding behaviour in F_3 generation: Non-fatuoid, Pubescence short	Non-fatuoid, Pubescence long	Fatuoid, Pubescence short	Fatuoid, Pubescence long	Remarks
904 Cn 5	Fatuoid; pubescence fairly short	20	—	—	15	—	Breeding true
7	,, ,,	10	—	—	6	—	,,
18	,, ,,	20	—	—	10	—	,,
22	,, ,,	4	—	—	2	—	,,
37	,, ,,	10	—	—	8	—	,,
904 Cn 17	Fatuoid; pubescence long	10	—	—	—	8	Breeding true
19	,, ,,	6	—	—	—	2	,,
20	,, ,,	20	—	—	—	10	,,
28	,, ,,	30	—	—	—	23	,,
904 Cn 11	Non-fatuoid; pubescence fairly short	10	7	—	—	—	Breeding true
25	,, ,,	30	21	—	—	—	,,
36	,, ,,	10	7	—	—	—	,,
904 Cn 13	Non-fatuoid; pubescence long	10	—	5	—	—	Breeding true
24	,, ,,	30	—	25	—	—	,,
45	,, ,,	7	—	6	—	—	,,
48	,, ,,	5	—	4	—	—	,,
904 Cn 38	Fatuoid; pubescence short	20	—	—	11	3	Homozygous fatuoid. Segregating for length of pubescence. Observed ratio 2·8 : 1. Expected 3 : 1.
40	,, ,,	5	—	—	3	2	
904 Cn 15	Non-fatuoid; pubescence short or fairly short	10	3	2	—	—	Homozygous Type A. Segregating for length of pubescence. Observed ratio 2·2 : 1. Expected 3 : 1.
44	,, ,,	30	13	7	—	—	
47	,, ,,	10	8	2	—	—	
904 Cn 2	Non-fatuoid; pubescence fairly long	10	—	5	—	1	Homozygous for long pubescence. Segregating for type of grain. Observed ratio 5 : 1. Expected 3 : 1.
8	,, ,,	10	—	6	—	1	
41	,, ,,	7	—	4	—	1	
904 Cn 1	Non-fatuoid; pubescence short or fairly short	50	25	—	7	—	Homozygous for short pubescence. Segregating for type of grain. Observed ratio 4·2 : 1. Expected 3 : 1.
9	,, ,,	20	13	—	2	—	
12	,, ,,	10	4	—	1	—	
29	,, ,,	30	13	—	3	—	
904 Cn 14	Non-fatuoid; pubescence short or fairly short	10	2	2	1	—	Segregating for both type of grain and length of pubescence. Observed ratio 8·7 : 3·7 : 2·0 : 1·0. Expected 9 : 3 : 3 : 1.
16	,, ,,	7	5	—	1	1	
30	,, ,,	6	3	2	—	1	
50	,, ,,	30	16	7	4	1	

parents of this cross, have invariably been recovered intact; and there is no evidence of their being other than dependent upon a single factor. A factor, however, which modifies length of pubescence from "long" to "short" is present in the fatuoid strain. This factor segregates independently of "type" of grain and gives therewith di-hybrid segregation. Its absence from the fatuoid genotype results in the appearance of fatuoids with long pubescence, whilst its presence in the Type A genotype gives Type A segregates with short pubescence. Two new genetical groups are therefore produced, namely, fatuoids with long pubescence and Type A grain with short pubescence; and these have occurred in their expected Mendelian frequencies.

It was further observed that when three-grained spikelets appeared in plants possessing Type A grain, the third grains were awnless, whereas third grains occurring in the spikelets of the fatuoid genotype were always awned.

(*g*) Strongly awned Type A (*ex* Ceirch-du-bach) × Ceirch-du-bach fatuoid.

Reciprocal crosses were made between the Type A and the fatuoid strains of Ceirch-du-bach in 1926, and two hybrid seeds, 1209 and 1210 Cn, were obtained. Both parents in this cross possess "long" basal pubescence and are morphologically identical in all plant characters except "type" of grain. The only contrasting characters to be dealt with, therefore, are the grain features of the Type A grain on the one hand, and of the fatuoid grain on the other (see Plate II, figs. 20 (*a*) and (*d*); also Plate I, figs. 11 and 13).

The F_1 *generation.*

As would be expected on analogy with the Type A × Supreme fatuoid cross described above, the spikelets and grain of the F_1 show close similarity to the Type A parent. The external resemblance is here even closer on account of the parents both possessing "long" pubescence. The pubescence on the rachilla of the fatuoid, however, is denser than that in the Type A strain; consequently, the hybrids show a slightly increased density as compared with the Type A parent. Apart from this the spikelets and grain of the hybrids and the Type A plants are practically indistinguishable. As in the previous crosses the characteristic features of the Type A grain are almost completely dominant over those of the fatuoid.

The F_2 *generation.*

In 1928, F_2 generations from the two F_1 plants 1209 and 1210 Cn were raised from seeds germinated in boxes in a cool greenhouse. Of the hybrids 200 and of each parent strain 10 seeds were sown, and germination in all lots was exceptionally good. The seedlings in general were of relatively uniform size and vigour, and almost all gave rise to well-developed plants. The data relative to the inheritance of the grain characters in this cross are shown in Table XII.

TABLE XII.

Description of parents and/or hybrid material	Reference numerals	No. of seeds sown	No. germinated	"Non-fatuoid"	Fatuoid
Parent lines:					
Type A (*ex* Ceirch-du-bach)	Cn 1113/2	10	10	All	—
Ceirch-du-bach fatuoid	Cn 1114/2	10	10	—	All
F_2 segregates:					
Fatuoid × Type A	1209 Cn	200	200	142	49
Expected on a mono-hybrid basis	—	—	—	143·25	47·75
Type A × fatuoid	1210 Cn	200	199	146	50
Expected on a mono-hybrid basis	—	—	—	147·00	49·00

Only two main kinds of segregates were distinguishable, namely:

(1) Segregates with grain like the fatuoid parent.

(2) Segregates with grain like the Type A parent.

As would be expected from the dominance of the Type A grain characters in the F_1 plants, discrimination between homozygous and heterozygous Type A segregates in the F_2 generation was not possible, and in Table XII the group consisting of the homozygous and of the heterozygous Type A plants is termed "non-fatuoid." From the data it is clear that we have here a case of simple mono-hybrid inheritance.

The line descendants of the respective parent plants remained uniform in type and general vigour, and continued throughout to breed true to their respective grain characteristics.

As in the cross Type A × Supreme fatuoid no segregates were obtained in which awns were absent from either the first or second or both these grains of the spikelets, or in which the lower grains possessed a glabrous and/or solidified base.

Despite a difference in density of pubescence on the rachilla between the two parental strains, all the extracted fatuoid segregates possessed the dense type of pubescence characteristic of the fatuoid type. There is no evidence of independent segregation, or of crossing-over, but the combined

features of the awn, pubescence and articulation of the two parental strains behave as simple allelomorphs.

(*h*) Strongly awned Type A × Scotch Potato fatuoid.

In this cross the parents differed in *colour* as well as in *type* of grain, the Scotch Potato fatuoid being white and the Type A parent black. Both parents, however, are similar in possessing the "long" type of pubescence (see Plate I, figs. 13 and 15, also Plate II, figs. 20 (*a*) and 22 (*d*), *left*).

Two hybrid seeds were produced in 1924 which were designated 908 Cn and 909 Cn, and these were grown as F_1 plants in 1925.

The F_1 *generation.*

In awn, articulation and pubescence and in colour of grain the F_1 plants of this cross are similar to those of cross (*g*) described above; that is to say, they resemble the Type A parent, differing from it only in the slightly denser pubescence of the rachilla.

The F_2 *generation.*

Fifty seeds from each of the two F_1 plants were sown singly *in situ* in 1926. But, as with all F_2 seed so sown in 1926, rather small plants were obtained and many casualties occurred. From 100 seeds sown, only 74 plants were available for grain investigation.

As in the Type A × fatuoid crosses already discussed, only two classes of segregates in respect of type of grain were distinguishable in F_2, namely, fatuoid and non-fatuoid, and these occurred in a 1 : 3 ratio (cf. Table XIII).

In respect of colour of grain the Type A parent was found to carry a factor for pale grey, hypostatic to the factor for black; the F_2 phenotypes therefore consisted of the three colour classes, black, pale grey and white. The pale grey and the white-grained plants have been grouped together in order to avoid any inaccuracy due to difficulties in distinguishing occasional single heads of immature grey grain, in which the colour was often not fully developed, from whites which have been slightly weathered. On this basis segregation was studied as between black and non-black colour and fatuoid and Type A grain, and the figures indicate a di-hybrid ratio. The double recessive is somewhat low, but the paucity of plants may reasonably account for that.

So far as the black and non-black colour classes are concerned there is no evidence of any linkage existing between colour and fatuoid or Type A kind of grain.

TABLE XIII.

Showing the F_2 segregation for type and colour of grain in two families of the cross strongly awned Type A × Scotch Potato fatuoid—1926.

Description of the cross	Reference numerals	No. of seeds sown	F_2 segregation: Non-fatuoid: Grain black	Non-fatuoid: Grain pale grey or white	Fatuoid: Grain black	Fatuoid: Grain pale grey or white	Total no. examined
Strongly awned Type A × Scotch Potato fatuoid	908 Cn	50	23	6	10	1	40
,, ,,	909 Cn	50	19	9	6	—	34
Totals	—	100	42	15	16	1	74
Calculated (9 : 3 : 3 : 1)	—	—	41·625	13·875	13·875	4·625	—
Observed ratio of non-fatuoid : fatuoid	—	—	57		17		—
Calculated (3 : 1)	—	—	55·5		18·5		—
Observed ratio of black : non-black =	—	—	58		16		—
Calculated (3 : 1)	—	—	55·5		18·5		—

$X^2=3{\cdot}265$. $P=0{\cdot}359$.

(*i*) *A.* STERILIS CULTA × *A.* SATIVA.

In 1922 a number of F_2 generation plants of crosses between *A. sterilis culta* (Marquand) var. Red Algerian and certain *A. sativa* varieties were examined for the presence or absence of dense, "tufted" pubescence at the base of the lower grain of the spikelets. These examinations were made on single-spaced plants at the time when the panicles were fully emerged, and while the plants were still growing in the field. After harvesting and threshing, determinations were also made of the type of articulation of the lower grains of the spikelet. During the collection of the latter data it became evident that all those plants previously classed as possessing dense, tufted, basal pubescence, possessed a basal articulation of the partially solidified type, and that the association between dense pubescence and partially or semi-solidified base was very definite. On the other hand, plants with little or no pubescence possessed either an intermediate or, more generally, a completely solidified base.

The segregates classified for basal articulation and basal pubescence appeared to fall into three main groups, two of which resembled the respective parental types, while the third was more or less intermediate, but resembling rather more closely the *A. sativa* parent, from which it could not invariably be distinguished. Of the type resembling the Red Algerian parent, most individuals agreed closely with the parental form in respect of articulation and pubescence, but some showed a slightly greater density of pubescence, and a slightly larger and less solidified basal cavity in the lower grains. The spikelets of these had a tendency to shed rather more freely when ripe. The actual breeding behaviour o these "transgressive" forms has not been critically studied, and it is not known whether they represent new genotypes or merely fluctuating forms of the parental type; for the present they have been included with the latter. Particulars of the crosses and the segregation of the grain characters in question are shown in Table XIV.

In columns 4 and 5 of this table the F_2 segregates are shown grouped into two main classes, namely, (1) those with dense pubescence and semi-solidified or partially solidified base, and (2) those with slight or no pubescence and with intermediate or solidified base. The former class represents the recessive "Red Algerian" phenotype, and the latter the grouped heterozygous and homozygous "*sativa*" classes. The crosses, which comprise hybridisations between the *A. sterilis culta* variety Red Algerian and the *A. sativa* varieties Grey Winter, Captain and Bountiful, all show good agreement with mono-hybrid segregation.

No observations were made on awn characters in relation to type of base in these particular hybrids.

TABLE XIV.

Showing the F_2 segregation of the characters dense basal pubescence and semi-solidified base in crosses between A. sterilis culta *var. Red Algerian and certain varieties of* A. sativa—1922

Particulars of the cross	Reference numerals	No. of plants investigated	F_2 segregation: Dense pubescence and semi- or partially solidified base	F_2 segregation: Slight or no pubescence intermediate or completely solidified base
*Grey Winter × Red Algerian	7 Cn	121	28	93
Red Algerian × Grey Winter	13 Cn	102	28	74
Totals	—	223	56	167
Calculated on a 1 : 3 basis	—	—	55·75	167·25
Red Algerian × Captain	12 Cn	158	36	122
* ,, ,,	31 Cn	166	47	119
Totals	—	324	83	241
Calculated on a 1 : 3 basis	—	—	81·0	243·0
*Red Algerian × Bountiful	14 Cn	272	64	208
Calculated on a 1 : 3 basis	—	—	68	204
Grand Totals	—	819	203	616
Calculated on 1 : 3 basis	—	—	204·75	614·25

* The observations in relation to basal pubescence in these families were made jointly by Mr C. V. B. Marquand, now of Kew Gardens, but formerly Officer in charge of Investigations in Oats at the Welsh Plant-Breeding Station, and the writer.

(*j*) *A. sterilis culta* var. Red Rustproof × *A. sativa* var. Scotch Potato.

This cross, which was made for the special purpose of studying the mode of inheritance of resistance to crown rust (*Puccinia coronata* Corda (6)), gave rise to a number of segregate grain-types in which the three characters semi-solidified base, dense basal pubescence, and *weak, non-twisted* awn were closely associated. For these characters the Red Rustproof parent appears to be genetically similar to Red Algerian, while Scotch Potato variety has a solidified base with very sparse or no pubescence, and the awns, which occur fairly frequently on the lower grains, are twisted and sub-geniculate, the upper grains being completely awnless.

From amongst a number of F_3 families of this cross, grown in 1926, 82 families were taken at random and classified for type of awn. They fell naturally into three main groups, viz. (1) those homozygous for twisted awn, (2) families segregating for twisted and non-twisted kinds

of awns, and (3) families homozygous for the weak, non-twisted awn. (1) showed also the basal articulation and pubescence of the Scotch Potato type; (3) resembled the weakly awned parent in this respect, while (2) showed an intermediate character. The number of families occurring in groups (1), (2) and (3) were 23, 42 and 17 respectively, a distribution agreeing fairly closely with expectation on a mono-hybrid basis.

In this cross, therefore, the two types of awns and their associated pubescence and articulation characters behave as simple contrasting allelomorphic groups, and no cross-over types were observed.

Coffman, Parker and Quisenberry (2), in a survey of variability in Burt oats, observed that the twisted awn was recessive to the weak non-twisted type, and believed the two kinds of awns to differ genetically. These authors also quote data from Wiggans (34) who, in a cross between Red Texas and Swedish Select, obtained simple Mendelian segregation between the strong, twisted and the weak, non-twisted types of awns. They also obtained a high correlation ($Q = 0{\cdot}909 \pm 0{\cdot}001$) between the semi-solidified base and the tufted basal pubescence.

An association between weak, non-twisted awns and medium-long pubescence has also been reported by Fraser (8) who, in a study of 2341 plants derived from a cross made between Burt and Sixty Day, obtained 5 per cent. of cross-overs. He also found the tufted pubescence, partially solidified base, and weak, non-twisted awn characters typical of the Burt variety to be recessive to the practically glabrous and solidified base and almost awnless condition of the Sixty Day variety and, apart from a few cross-overs, to segregate as a simple recessive group of characters.

There is here, therefore, evidence of an association between basal pubescence, semi-solidified base and the *weak, non-twisted* awn as distinct from the association of basal pubescence, semi-solidified base and *strong, twisted* awn as in the Type A and the Type B plants described above (see pp. 12–14).

In general, it may be concluded from these studies, that a definite association exists between awn, articulation and pubescence in *A. fatua*, in fatuoids, and in the several aberrant forms occurring in the species *A. sativa* and *A. sterilis culta* and their hybrids.

VI. DISCUSSION.

We may now discuss these fresh facts in connection with the three hypotheses mentioned earlier (cf. p. 5).

The natural crossing hypothesis.

Against this hypothesis is the opinion generally held, which is supported by evidence, that the *A* series fatuoids differ from the varieties in which they arise only in the type of articulation, pubescence and awn development of the grain.

Such defined and delimited characteristics, as Nilsson-Ehle (18) and Åkerman (1) maintain, would not invariably occur if fatuoids originate by natural crossing with *A. fatua*, for in such cases other plant characters would be introduced by the cross, and the resulting natural hybrid should show complex rather than simple segregation as generally occurs.

As demonstrated by Surface (21) in artificial crosses between *A. fatua* and *A. sativa* var. Kherson, by Crépin (3, 4, 5) in natural hybrids between *A. fatua* and Golden Rain, and by Tschermak (23) in crosses between *A. fatua* and cultivated oats, complex segregation in respect of colour of grain, hairiness of the outer paleae and other plant features occurs in addition to the simple segregation in respect of the linked characters articulation, basal pubescence and awn.

And further, if as Zade (26) contends, the observed hybrid may not be F_1 but F_n, it is still difficult to see how in the case of a heterozygous fatuoid, such as that of the variety Golden Giant, which is yellow in colour of grain, unilateral in type of panicle and eligulate, should, as a result of natural crossing with *A. fatua*, segregate into homozygous fatuoids, intermediates and normals, in respect of type of grain, and yet remain true-breeding and identical with the type variety in respect of unilateral panicle, absence of ligule and other varietal features.

That natural crossing in oats does occasionally occur is generally admitted, but the examples recorded in the present paper, namely, the *Avena nuda* hybrid and the two black-grained fatuoids in the cross Victory × Red Algerian, support Nilsson-Ehle's contention that such natural hybrids, when they do occur, show segregation in respect of plant characters other than, and additional to, those which characterise the respective fatuoid and normal types of grain. The fatuoid or *fatua*-like segregates of such natural hybrids are seldom, if ever, identical with the mother plant in general morphological characters, and this feature in itself stamps such forms as products of natural crossing and distinguishes them from spontaneous heterozygous fatuoids; for in the latter, the characters by which they differ from the normal or type variety are solely the associated characters of awn, articulation and pubescence, and these are closely, if not absolutely, linked in inheritance.

Further, as a possible interpretation of the sub-fatuoid and various "awned" types, the natural crossing hypothesis is still less satisfactory, for here the aberrant forms are completely different in grain characters from either normal *A. sativa* or typical *A. fatua* plants. At the same time, and like the true fatuoid oat, both the strongly awned Type A and the Type B strains differ from their respective mother plants only in awn, articulation and pubescence, and these characters have been shown to behave in inheritance as simple, linked and recessive units in relation to the normal *A. sativa* type of grain, and as almost completely dominant units in relation to the fatuoid kind of grain. The fatuoid and "awned" types appear to be simple allelomorphs in relation both to normal grain and to one another.

As an interpretation of the mode of origin, of the sub-fatuoid and "awned" forms as well as of *A* series fatuoids, the natural crossing hypothesis appears to the writer to be wholly untenable.

The mutation hypothesis.

According to this hypothesis, as stated by Nilsson-Ehle (18), the initial heterozygous fatuoid arises through complex gene mutation in one of the germ cells, and gives, in combination with the normal type grain, simple Mendelian segregation. The fatuoid complex behaves accordingly as a simple gene. On this basis, the fatuoid should resemble the seed parent in all plant characters except those affected by the mutation, and this is exactly what has been generally found to occur. The cause of origin of the fatuoid heterozygotes, as Nilsson-Ehle maintains, can under no circumstances be sought *outside* the strains in which they occur, but must be present in the genetical constitution of the specific lines producing the fatuoids.

On analogy with speltoid wheats, Nilsson-Ehle considers that dissociation of the fatuoid gene-complex may occur, and that examples may appear in which the fatuoid awning occurs without the horseshoe-shaped base, and conversely the fatuoid base without the fatuoid awn.

Gante (9) found plants with individual spikelets which showed awning on the second as well as on the first grains, and appeared to be examples of the kind expected by Nilsson-Ehle; but when studied the awning of the second grain proved to be of a fluctuating character, and was not inherited by the progeny. Such plants and awn behaviour resemble to some extent those of Type D described above (see p. 16).

The true-breeding Type A and Type B plants described in the present paper (see pp. 12–16) appear to support Nilsson-Ehle's position. In

these the strong, twisted and geniculate awns occur on both the primary and the secondary grains, and the horseshoe-shaped base is absent. But whether these forms should be considered as being actually due to the dissociation of the factors of the fatuoid complex is a point which is dealt with later.

For the fatuoid, sub-fatuoid and strongly awned types, the mutation hypothesis agrees closely with the experimental facts; for by mutations of varying degree in the "normal" type chromosome of a particular gamete, and by the pairing of this chromosome with a "normal" type chromosome at fertilisation, a fatuoid, sub-fatuoid or strongly awned heterozygote could arise which, in the following generation, would segregate into homozygous mutant, heterozygous mutant and normal types in a simple Mendelian manner.

There is, however, a difficulty when this hypothesis is applied to fatuoids of the *B* series group. In the heterozygous fatuoids of this series, only 41 chromosomes are present (one of the "normal" chromosomes being missing), and by the random distribution of the odd ("normal") chromosomes, in meiosis, gametes possessing 20 and 21 chromosomes respectively are produced. These, according to Huskins, give rise to zygotes with 40, 41 and 42 chromosomes, corresponding to the fatuoid, intermediate and normal phenotypes. In the absence of the "normal type" chromosome—which is the one that on Nilsson-Ehle's hypothesis gives rise by mutation to fatuoids—homozygous fatuoids are produced. Fatuoids occur in the absence of the "normal" chromosome pair, and this is a serious obstacle to the general and straightforward application of a simple mutation theory. This aspect of the problem, however, will be further considered when the chromosome aberration hypothesis has been discussed.

The chromosome aberration hypothesis.

The chromosome aberration hypothesis, as applied by Huskins (14) to the interpretation of the origin of fatuoids in oats, was first put forward by Winge (25) in explanation of the origin of speltoids in wheat. The analogy between the occurrence of speltoids in wheat and of fatuoids in oats has been discussed by Huskins (14, 15), whose researches into the cytology of a number of these forms have convinced him that a causal relationship exists between chromosome numbers and cytological behaviour on the one hand, and of the spasmodic appearance of these aberrant forms on the other. The hypothesis involves a consideration of the phylogeny of the species concerned.

Both *Triticum* and *Avena* show three main groups of species, viz. diploid, tetraploid and hexaploid, with 7, 14 and 21 pairs of chromosomes respectively.

Winge (25) represents the hexaploid species as originating by the triplication of the chromosomes of an original diploid species, and as carrying in the haploid condition three sets of each of the seven basic chromosomes. The somatic complement in the hexaploid thus consists of seven di-triploid groups of chromosomes, each group being made up of three pairs of homologous chromosomes which, for convenience, he represents by the formula $\frac{ABC}{ABC}$. It is conceded that these three pairs of chromosomes are not strictly identical, B being regarded as possessing genes or determinants for the speltoid characters, and C for the normal *T. sativum* characteristics. The presence of the C-chromosome pair restricts any expression of the speltoid characters carried by the B pair. In other words, the distinguishing characters of C are epistatic to those of B. By the normal pairing of A with A, B with B, and C with C, the equilibrium of the $\frac{ABC}{ABC}$ di-triploid group is maintained, and a true breeding progeny is assured; but if faulty pairing between the B and C chromosomes should occasionally take place, gametes of the type ABB and ACC may be formed. Thus the pairing of ABB with a normal (ABC) gamete would give rise to the initial heterozygous speltoid genotype which would segregate into the three zygotic combinations $\frac{ABC}{ABC}$, $\frac{ABB}{ABC}$, $\frac{ABB}{ABB}$ (representing respectively the homozygous normal, heterozygous speltoid and homozygous speltoid genotypes), and these would occur in the numerical proportions of 1 : 2 : 1. The odd B-chromosome in conjunction with the odd C-chromosome in the heterozygote simulate in inheritance the behaviour of a single factor. The A-chromosome is considered to divide in a regular and normal manner, but by the faulty pairing of B and C various univalent, trivalent and quadrivalent chromosome arrangements occur. Moreover, and accompanied by more complex and irregular cytological conditions, other speltoid types may arise with chromosome complements deviating from the normal $2n = 42$, number by one or more chromosomes, plus or minus. The "di-triploid group" in such cases presents excess or deficiency of either B or C, and such forms are highly variable in vigour and fertility. In their breeding behaviour they give rise to very irregular genetical ratios.

In the application of this hypothesis to the closely analogous problem of the origin and production of fatuoids in oats, Huskins (14) has introduced certain modifications. The di-triploid constitution of the hexa-

ploid species is accepted, but its mode of origin as applied to the *Avena* species is differently explained. Instead of direct triplication of an original diploid set of chromosomes it is maintained that the hexaploid species have arisen "through the hybridisation of a tetraploid with another diploid species." This means that the di-triploid set consists of chromosomes from two or even three different ancestral species, depending upon whether the original tetraploid parent possessed chromosomes of similar or dissimilar specific origin in its di-diploid set. The hexaploid formulae on the former assumption (two ancestral species) is given as $\frac{S_1S_2F}{S_1S_2F}$, and on the latter (three ancestral species) as $\frac{XSF}{XSF}$, in application to the species *A. sativa*.

The basic difference between the formulae of Huskins and of Winge is that of the time at which the minor differences in the separate chromosome pairs of the di-triploid set arise. Huskins' hypothesis implies that these differences existed in the ancestral diploid and tetraploid species, while Winge conceives of a single diploid species giving rise to a hexaploid by direct triplication. In this latter case, all three pairs of chromosomes in the di-triploid set must at their inception have been truly identical, and in the subsequent course of descent have diverged either by inherent germinal change or by natural hybridisation with one or more species of presumably a separate line of descent. This consideration raises the interesting points of whether the factorial differences which exist between the separate pairs of the di-triploid set are of recent or of remote origin, of the constancy of these germinal differences, and of the relative frequency of appearance in them of factor mutations. These points, however, need not be discussed here.

More recently Huskins (15) uses the symbols $\frac{ABC}{ABC}$ in preference to $\frac{XSF}{XSF}$ or $\frac{S_1S_2F}{S_1S_2F}$ for the di-triploid chromosome group concerned, and these symbols will therefore be used in the present discussion. C now represents a chromosome carrying the factors which determine the *sativa* or normal grain characters, and B the chromosome which carries factors concerned with fatuoid or *fatua* features of the grain. Accordingly the formulae for the heterozygous fatuoids of the A series will now be $\frac{ABC}{ABB}$; for heterozygous fatuoids of B series $\frac{ABC}{ABo}$; and for heterozygotes of C series $\frac{ABC}{ABCB}$.

Fatuoids of A *series*. In the pollen mother-cells of the A series group, 42 chromosomes forming 21 pairs are stated to be a regular feature of the normal segregates, while the arrangement in the heterozygous fatuoid

is frequently 19 pairs, 1 trivalent and 1 univalent, and that in the homozygous fatuoid, 19 pairs and 1 quadrivalent. The presence in the heterozygote of a trivalent and a univalent in the same cell is, however, rarely found, and its demonstration appears to be a matter of much difficulty, especially in fatuoids of the *A* series group. Their occurrence, however, is fundamental to this hypothesis, especially in relation to fatuoids of the *A* series group.

From a comparison of the cytology of the three segregate types, namely $\frac{ABC}{ABC}$, $\frac{ABC}{ABB}$ and $\frac{ABB}{ABB}$, it was found that characteristic irregular chromosome arrangements occurred fairly frequently in the $\frac{ABC}{ABB}$ and $\frac{ABB}{ABB}$ genotypes, quadrivalents in the latter, trivalents and univalents in the former, in place of the normal arrangement of 21 conjugating pairs, but they were not of general occurrence.

According to Huskins "an occasional aberration (probably the formation of a quadrivalent) in the meiotic division of normal cultivated oats produces a gamete in which one particular chromosome-bearing *fatua* or fatuoid character is duplicated and another bearing normal type factors is absent. The union of this gamete with a normal one would produce a Type 1" (that is, an *A* series) "heterozygous fatuoid."

Such a hypothesis carries with it certain theoretical and practical implications. In the first place, if the equilibrium of the $\frac{ABC}{ABC}$ chromosome group is disturbed by faulty pairing between *B*- and *C*-chromosomes resulting in univalents and trivalents being formed, individuals deviating from the normal 42 chromosome complement should, owing to this irregularity, be expected occasionally in some at least of the ensuing progeny. It is, however (and by Huskins' definition), a characteristic of all the genotypes of this series that they possess 42 chromosomes, and this, it should be emphasised, in spite of the fact that whole chromosome differences between fatuoid and normal segregates are postulated, and that the odd *B*-chromosome of the heterozygote must either (1) pair with *C*, (2) remain unpaired, or (3) form a trivalent with the *B* pair of chromosomes, leaving *C* as an unpaired individual; while, moreover, it is held to be a condition of the constancy of equilibrium of the normal di-triploid group that *A* pairs with *A*, *B* with *B* and *C* with *C*.

Further, only three examples of irregularities such as excess or deficiency in chromosome numbers in fatuoids are on record, namely, the two strains described by Huskins and the one found by Goulden. These have been classed by Huskins as fatuoids belonging to the *B* and *C* series groups. Such forms are of rare and exceptional occurrence, show

abnormal segregation ratios, and are accompanied by dwarfness and sterility in all the members of the homozygous fatuoid genotypes.

Secondly, on grounds of analogy, one would expect that some at least of the six remaining di-triploid groups of chromosomes would behave in a similar way, that is, they also should occasionally show faulty pairing between their respective semi-homologous chromosome pairs. But on the assumption that all examples of univalents, trivalents and quadrivalents in the cells in the genotypes under consideration are alone concerned with the fatuoid phenomenon, it appears to be assumed that they do not.

Thirdly, it is stated that the formula "applies to fatuoids which are similar to the variety in which they occur in all respects excepting those comprising the fatuoid complex." The hypothesis therefore implies that the "*C*"-chromosome pair differs from the "*B*" pair only in the factor, or factor complex, affecting articulation, pubescence and awn development, and that the factor or factors for other plant characters, if any, borne by the *B*- and *C*-chromosome pairs are genetically identical, and therefore apparently interchangeable without causing change or modification of any other genetical features of the plant.

The fatuoid type described in the present paper as occurring in the variety Golden Rain could not, therefore, be included in the *A* series category—although the phenotypes are of equal vigour, as indicated by height and number of culms, and also carry, in all probability, the normal chromosome complement. To include this form with the *A* series it would be necessary to admit that the *B* chromosome differs from *C* in respect of a factor for spikelet production.

Further, in respect of the sub-fatuoid oat we must either have recourse to mutation to supplement the chromosome aberration theory in order to provide a satisfactory explanation of the origin of this type, for in this oat the spikelets differ from the common fatuoid type by a small inherited difference affecting floret articulation, or we must assume that the *B*-chromosome of this strain differs from the *B*-chromosome of practically all varieties which hitherto have given rise to fatuoids.

Fatuoids of B *series.* In connection with the fatuoids of *B* series, on the other hand, there is, as very clearly demonstrated by Huskins, a marked correlation between the irregular cytological behaviour and chromosome numbers on the one side, and genetical ratios and phenotypical vigour on the other. The complete absence of the *C*-chromosome pair results in the production of homozygous fatuoids of sub-normal vigour and stature, possessing rather fewer spikelets, most or generally

all of which are sterile, and in which irregular segregation ratios occur. It is evident that the segregation ratio is here very probably associated with the chance distribution of the odd chromosome in the heterozygote, and the chromosome aberration hypothesis undoubtedly offers an adequate interpretation of the observed phenomena.

Fatuoids of C *series.* Here the chromosome aberration hypothesis also meets the case, for whole chromosome differences are a regular occurrence, and the irregular genetical ratios are such as would be expected to arise where very irregular cell-divisions occur.

Such evidence suggests that the chromosome aberration hypothesis as outlined by Huskins has limitations, especially in its application to *A* series fatuoids, which, from their relative abundance, constitute the main fatuoid problem. The hypothesis therefore cannot be held to be a satisfactory elucidation of the main problem at issue; it certainly fits the exceptional cases, the *B* and *C* series fatuoids, remarkably well, but the regular occurrence of 42 chromosomes in all phenotypes of *A* series fatuoids, and the equal vigour of all the segregates, are not features which would be expected normally to accompany phenomena arising by chromosome irregularity. Moreover, the demonstration of a factor for low spikelet number, behaving as a linked unit in relation to the fatuoid complex in the Golden Rain fatuoid, is evidence of the occurrence in the *B*- and *C*-chromosomes respectively of factors other than those determining or restricting the fatuoid complex. Hence to accept the chromosome aberration hypothesis, we must assume that all fatuoids hitherto described have *B*- and *C*-chromosomes possessing similar factors for spikelet production, and also that in the course of their recent descent, *i.e.* from their inception as polyploids, they have undergone parallel genetical variations; for it must be admitted that in so far as spikelet producing capacity is concerned the numerous varieties of *A. sativa* show very marked characteristic and inherent differences.

To take the case of the fatuoid of Fulghum, a variety possessing *A. sterilis culta* characteristics—the marked similarity between the normal and fatuoid segregates in spikelet production and their general agreement with the parent variety in all plant characters except type of grain is exactly parallel with the behaviour and characteristics of *A* series fatuoids of *A. sativa* varieties. This, however, is the more remarkable if, as Huskins (13) contends, the cultivated variety Fulghum probably originated relatively recently by natural crossing with *A. sativa*, and the origin of its *B*-chromosome is due to this cause. Under such circumstances the *B*- and *C*-chromosomes would be expected to carry dis-

similar factors in respect of the spikelet-producing character. *A. sativa* varieties generally possess a higher average number of spikelets per plant than do members of *A. sterilis culta*; it would therefore be reasonable to expect the *B*-chromosome in Fulghum to carry a factor or factors for spikelet number different from that carried by the *C*-chromosome of this variety; and on the chromosome aberration hypothesis the extracted fatuoid and normal segregates should show linked differences in respect of spikelet-producing capacity. There is, however, no evidence of this in the progeny of the Fulghum fatuoid × normal cross (see Table VI, p. 33).

Further evidence of the lack of identity between the *C*-chromosome of *A. sativa* and the *C*-chromosome of *A. sterilis culta*, apart from the factor or factors which determine their main species distinguishing characters, is provided by the occurrence in the *C*-chromosome of the latter of a factor which converts the strong, twisted awn characteristic of fatuoids, and of *A. fatua*, into a weak, non-twisted awn. This factor is possessed by, and peculiar to, certain *A. sterilis culta* strains, whilst it is absent, for instance, in *A. sterilis maxima*.

These details add considerably to the difficulty of assuming that similarity between the *B*- and the *C*-chromosomes which is involved in the chromosome aberration hypothesis as at present elaborated.

The sub-fatuoid and true-breeding, strongly awned types. It is, however, when considered in relation to the origin of the sub-fatuoid and the Type A and Type B strains, that the general inadequacy of the chromosome aberration hypothesis is most apparent. Although not put forward in explanation of such types, owing to presumed fundamental differences in respect of their mode of origin, the data reported in the present paper nevertheless demonstrate the allelomorphic nature of the fatuoid and strongly awned types, and the close relationships that exist between the several aberrant forms. Like fatuoids, the sub-fatuoid and true-breeding "awned" types show the same general inherited characteristics, in that they differ from the normal by a single factor-complex which behaves as a simple unit in inheritance, while in other plant-characters they show complete similarity with the mother plant from which they arise. These features, presumably, may be held to indicate that the factors which determine the different aberrant forms, both fatuoid, sub-fatuoid and awned types, are located in one and the same chromosome, and that these several types have a similar and related mode of origin. There appears, therefore, to be no justification for explaining the origin of fatuoids by chromosome aberration, and of strongly awned types by crossing-over and/or factor mutation.

Moreover, certain theoretical considerations are opposed to the acceptance of Huskins' suggestion that the origin of the true-breeding, strongly awned types—*e.g.* the Type A form—may be due to crossing-over between "semi-homologous" chromosomes. This mode of origin implies the pairing of a *B*- with a *C*-chromosome, and of the occurrence of crossing-over between them. Pairing of this kind, however, has been suggested by the same author as being instrumental in the production of heterozygous fatuoids; this being so, and on the basis of the crossing-over hypothesis, these strongly awned forms should occur in some definite percentage frequency in the progeny of this genotype, and also always in conjunction with the latter. The data obtained in this investigation give no evidence of their occurrence in this way, for neither the sub-fatuoid nor any of the strongly awned types have arisen in conjunction with fatuoids.

In explanation of the origin of the strongly awned types, we are, therefore, left with Huskins' alternative hypothesis of factor or gene mutation. But if the mutation hypothesis is a satisfactory explanation of the origin of these, and the data support this view, we might quite reasonably ask: Why adopt a mutation hypothesis in respect of the true-breeding "awned" types and a chromosome aberration interpretation in respect of fatuoids, seeing that fatuoid, sub-fatuoid and "awned" types are related phenomena and behave one to another as allelomorphic units?

There is, however, an obstacle to the general application of Nilsson-Ehle's mutation hypothesis which has already been referred to above, viz. the occurrence of homozygous fatuoids in the absence of the "normal" chromosome pair. This difficulty, however, is more apparent than real, depending upon our interpretation of the action and inter-action of the genetic factors, and of the constitution of the general chromosome complement.

If, instead of the former belief (upon which the present mutation hypothesis in relation to fatuoids was based) that the cultivated varieties of oats possess 21 diploid chromosomes, we accept the newer theory of the polyploid origin and di-triploid chromosome constitution of the 42 chromosome species as formulated by Huskins in relation to his chromosome aberration hypothesis, the difficulty of explaining the origin of fatuoids in the absence of the "normal" chromosome pair disappears. For on this interpretation the factor or factors which determine fatuoid type of grain on the one hand, and normal type on the other, are assigned to separate chromosome pairs which we may call the "fatuoid" and "normal" chromosome pairs respectively; the factors in the normal

chromosome being epistatic to those in the fatuoid chromosomes. Accordingly, the complete loss of the "normal" chromosome pair (as in the B series homozygous fatuoid) is equivalent, in so far as articulation, pubescence and awn characters are concerned, to a latency or loss mutation of the factor or factors which determine normal type of grain. Hence, in the absence of the "normal" chromosome pair, we should expect to obtain plants of homozygous fatuoid phenotype.

The "fatuoid" and "normal" chromosome pairs, however, probably carry factors other than, and additional to, those affecting awn, articulation and pubescence, and therefore, in the absence of the "normal" chromosome pair, associated differences between the fatuoid and normal segregates in characters other than those mentioned would be expected to appear. Actually there occurs in the B series group (and in the C series also) a reduction in height, tillering capacity and spikelet numbers, and a general lack of vigour and fertility, associated with the fatuoid genotype; but to what extent these associated differences are wholly, or even partly, due to the absence of the "normal" chromosomes, or to the unbalanced condition of the cell arising through chromosome disarrangement and deficiency, it is difficult to say. It is apparent that the "fatuoid" and "normal" chromosomes carry factors other than those which determine the fatuoid and normal types of grain, and that they are in consequence not interchangeable in the sense demanded by the chromosome aberration hypothesis. To bring these facts into line we suggest the following hypothesis.

A modified mutation hypothesis.

If we accept the polyploid origin of the species in question, and adopt the formula $\frac{ABC}{ABC}$ employed by Huskins to denote the particular di-triploid chromosome group concerned with the fatuoid phenomena, we may conceive of the origin of the several aberrant grain types discussed above in the following manner.

Assuming the B-chromosome to carry factors, amongst others, for fatuoid or *fatua* type of grain and for low spikelet numbers, and C to carry factors for normal or *sativa* type of grain, and for high spikelet numbers—the factors of C being epistatic to those of B—then, the occurrence of a factor mutation in C would unmask its hypostatic factor counterpart in B, and so give rise to grain types characteristic of and inherent in B. The extent to which factors borne by B would find expression would depend upon the nature and extent of the mutation occurring in C.

Thus by mutations of different degrees of complexity in C, which we may designate C_1, C_2, C_3, etc., the several heterozygous mutant types would arise; for example, $\frac{ABC}{ABC_1}$ might represent one type of mutant heterozygote, $\frac{ABC}{ABC_2}$ another type and $\frac{ABC}{ABC_3}$ still another type; all of which would show simple segregation in relation to the normal type of grain, behave as simple allelomorphs in relation one to another, and give simple segregation on inter-crossing.

On account of specific differences between the C-chromosomes of *A. sterilis culta* and *A. sativa* respectively, and of the existence of closely parallel mutations within the two species, it would be necessary to make a distinction between the formulae for these two species. We may therefore represent the particular di-triploid group concerned in the *A. sterilis culta* species by the formula $\frac{ABD}{ABD}$, and confine the formula $\frac{ABC}{ABC}$ to members of the *A. sativa* species.

Accordingly, for the various mutant forms so far observed in *A. sativa*, the respective formulae for the *heterozygous* individuals, in order of increasing complexity, would be:

For the strongly awned Type A	$\frac{ABC}{ABC_1}$
For *A* series fatuoid	$\frac{ABC}{ABC_2}$
For Golden Rain fatuoid	$\frac{ABC}{ABC_3}$
For the *B* series fatuoid	$\frac{ABC}{ABo}$

Similarly, in respect of somewhat parallel forms arising in the species *A. sterilis culta*, the formulae for the heterozygous plants would be:

For Type C	$\frac{ABD}{ABD_1}$
For weakly awned	$\frac{ABD}{ABD_2}$
For Type B	$\frac{ABD}{ABD_3}$
For sub-fatuoid	$\frac{ABD}{ABD_4}$
For the *A* series fatuoid of Fulghum ...	$\frac{ABD}{ABD_5}$
For the *B* series fatuoid	$\frac{ABD}{ABo}$

The C series heterozygous fatuoids in *A. sativa* varieties would, on this basis, be denoted by $\frac{ABC}{ABBC}$ or $\frac{ABC}{ABC_2C}$, and of *A. sterilis culta*, by $\frac{ABD}{ABBD}$ or $\frac{ABD}{ABD_5D}$.

Hence it follows that the factors for awn, articulation and basal and

rachilla pubescence are located in the *B*-chromosome pair, and that the extent to which any or all of these find phenotypical expression depends upon the presence or absence of their epistatic counterparts in the *C*- or *D*-chromosome pair.

So also the weak, non-twisted awn which is of frequent occurrence in *A. sterilis culta* varieties depends upon the same basic "awn factor" as the awn in *A. sativa* varieties, but its expression as a weak non-twisted awn in the normal and heterozygous fatuoid segregates is due to a factor or factors present in the *D*-chromosome. This conclusion arises from the study of the crosses Fulghum fatuoid × normal and Fulghum fatuoid × Grey Winter (*A. sativa*) normal.

Hence, the fatuoid awn, the so-called cultivated awn of *A. sativa* varieties, and the weak, non-twisted awn of *A. sterilis culta* varieties are all individually dependent upon this same basic "awn factor," and the phenotypic expression of the awn as a "fatuoid" awn, a "cultivated" awn, or a "non-twisted" awn depends upon the presence or absence of epistatic and/or modifying factors carried by the *C*- or *D*-chromosomes, as the case may be.

Raum and Huber (19) found that the awning frequency in the heterozygous fatuoid and homozygous normal genotypes showed distinct variations from season to season, awns being most frequent when low rainfall coincides with the time when the awn primordia are laid down; but they found no such variations to occur in the homozygous fatuoid awn. They concluded that the "restricting" gene (*Hemmungsgen*) of the awning is influenced by external conditions, but that the "awn" gene (*Grannengen*) is not affected. A distinction is thus made between a basic or "awn" gene, and a modifying or "restricting" gene.

Pubescence is fundamentally deemed to be of the long, dense, bushy type as seen in those fatuoids with long pubescence. In the normal and the heterozygous fatuoid genotypes, the *density* of the pubescence is generally modified and restricted by factors occurring in the *C*- (*A. sativa*) or *D*- (*A. sterilis culta*) chromosomes. Its *length*, however, is governed by at least one factor which, when present, reduces the pubescence from "long" to "short." This factor is inherited independently of the fatuoid and normal grain-type characters.

The form of articulation, or attachment of the spikelets and florets, is regarded as being fundamentally of the *fatua* or fatuoid type, and its factors hypostatic to those determining normal attachment in *A. sativa* and *A. sterilis culta* varieties.

Briefly the basic awn type seems to be the fatuoid or *fatua* type; the

basic articulation, the horseshoe form; and the basic pubescence, the long, dense, bushy type. These three characters are closely, if not absolutely, linked, and constitute the basic *fatua* or fatuoid character complex. In the grain of cultivated varieties of both *A. sativa* and *A. sterilis culta* species their phenotypical expression is variously affected by the presence or absence of epistatic or modifying factors, *mainly* located in the *C*- or *D*-chromosomes. These latter determine the varied expressions of awn, articulation and pubescence met with in the several cultivated varieties of these two species, and mutations in them probably determine the various aberrant fatuoid, sub-fatuoid and strongly awned types of *A. sativa* and *A. sterilis culta.*

VII. SUMMARY

Nine fatuoids are described which were found in commercial varieties of oats. Those present in Fulghum, Orion, Ceirch-du-bach, Scotch Potato and Royne, possessed long basal pubescence, whilst those occurring in Cornellian, Golden Giant and Record had distinctly short pubescence. From the breeding behaviour of the heterozygotes and the general vigour of the fatuoid intermediate and normal segregates, these several varietal forms appear to belong to the *A* series group (Huskins' classification).

In Golden Rain a fatuoid was found differing from the normal strain in spikelet number as well as in type of grain. The extracted segregates in this form showed definite association between fatuoid grain and low spikelet number. This fatuoid has been previously shown (16) to differ from the normal in the absence of yellow colour in the grain, and consequently differs widely from fatuoids of the *A* series type.

Fatuoids are also described which appeared in the F_3 and F_4 generations of artificial crosses between *A. sterilis culta* and *A. sativa*, and between the latter species and *A. nuda*. These all agree in general external characters with fatuoids of the *A* series type. Two of the specimens originated by natural crossing with other fatuoid plants in the F_1 generation; the remainder probably by mutation.

A peculiar sub-fatuoid mutant is described from an F_4 family *ex* Red Algerian × Golden Rain. This breeds true to its characteristic type of partially disarticulating florets and freely shedding spikelets.

True-breeding strongly awned and other types differing variously from typical fatuoids were found in Ceirch-du-bach and Norwegian Grey oats, and in the progenies of Victory × Red Algerian and Red Algerian × Scotch Potato. Four types, designated Types A, B, C and D respectively, were distinguished and separately considered.

Crosses between fatuoids and normal strains of several varieties, between fatuoids and certain strongly awned types, and between fatuoids of the species *A. sativa* and *A. sterilis culta* were studied, and the records point to simple allelomorphic relationships between the several abnormal forms.

The partially solidified base, basal pubescence and weak, non-twisted awn characteristic of certain *A. sterilis culta* strains are shown to be associated in inheritance, and to behave as a simple allelomorphic group to the normal. The weak, non-twisted awn is probably genetically similar to the strong, twisted awn, its characteristic phenotypical expression being due to the presence of a modifying factor carried by the "normal" or *D*-chromosome in certain *A. sterilis culta* strains.

A simple factor modifying length of pubescence in the fatuoid oat was found to be inherited independently of either fatuoid or Type A kind of grain.

Factors for black and non-black colour of grain showed independent segregation in relation both to fatuoid and to Type A grain.

The cross Fulghum (*A. sterilis culta*) fatuoid × normal, and reciprocal, like crosses of fatuoid × normal of *A. sativa* strains, gave only simple segregation; the fatuoid line plants invariably bred true.

Fulghum fatuoid × Grey Winter (*A. sativa*) normal also gave unifactorial segregation.

With the exception of five plants which were probably natural hybrids, Fulghum fatuoid × Golden Rain (*A. sativa*) fatuoid gave nothing but fatuoids in F_1 and F_2. A very high proportion of empty grains, however, occurred in the F_1 plants.

Avena nuda fatuoid × Scotch Potato normal gave approximately monohybrid segregation, but agreement with expectation was not very good.

In crosses between Ceirch-du-bach, Supreme and Scotch Potato fatuoids, and the Type A strain of Ceirch-du-bach, there was no break-up of the associated characters, horseshoe-shaped base, pubescence and awn of the fatuoids on the one hand, and of the partially solidified base, pubescence and awn of the Type A grain on the other.

The three main hypotheses of the origin of *A* series fatuoids are discussed with special reference to fatuoids, sub-fatuoids and the various strongly awned types, and a number of theoretical and practical limitations pointed out.

Genetical differences between the respective "normal" chromosomes of *A. sativa* and *A. sterilis culta* are demonstrated and discussed, and

separate formulae are given for the somewhat parallel series of mutations that were found to occur within these two species.

A modified mutation hypothesis of general application to fatuoids as well as to the various sub-fatuoid and true-breeding "awned" types is submitted in place of the chromosome aberration hypothesis.

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EXPLANATION OF PLATES.

Plate I.

(All figures much enlarged.)

Fig. 1. Ventral view of lower grain of the sub-fatuoid mutant oat, showing horseshoe-shaped articulation, short pubescence and a basal fracture of the rachilla (as in *A. sterilis culta*)—see also Plate II, fig. 21 (b).

Fig. 2. Dorsal view, ditto.

Fig. 3. Dorsal view of sub-fatuoid second grain, showing pubescence and attachment of the rachilla.

Fig. 4. Ventral view of sub-fatuoid second grain, showing the partial articulation surface, or cleavage plane, at the apex of the adhering rachilla of the primary grain.

Fig. 5. Ventral view of the base of the sub-fatuoid second grain (third grain attached above), showing apical fracture of the rachilla and the basal cavity.

Fig. 6. Ventral view of lower grain of Type B mutant, showing sem-solidified basal articulation, basal pubescence and a basal fracture of the rachilla—see also Plate II, fig. 21 (*c*) (*left*).

Fig. 7. Dorsal view, ditto.

Fig. 8. Ventral view of second grain with rachilla of primary grain attached. Note complete absence of any cleavage or articulation surfaces and the complete confluence of the rachilla with the base of the second grain.

Fig. 9. Dorsal view, ditto.

Fig. 10. Ventral view of the base of a spikelet of Type D, showing a fairly completely solidified base (as in *A. sativa*) and complete absence of pubescence—see also Plate II, fig. 22 (*c*).

Fig. 11. Ventral view of a fatuoid of the variety Ceirch-du-bach (*A. sativa*), showing horseshoe-base and long pubescence—see also Plate II, fig. 20 (*d*).

Fig. 12. Ventral view of a lower grain of normal Ceirch-du-bach—see also Plate II, fig. 20 (*c*).

Fig. 13. Ventral view of a lower grain of Type A mutant of Ceirch-du-bach. Note semi-solidified basal articulation and long and fairly dense pubescence—see also Plate II, fig. 20 (*a*).

Fig. 14. Ventral view of a fatuoid showing "short" pubescence.

Fig. 15. Ventral view of a fatuoid showing "long" pubescence.

Plate II.

(Figs. 16–19 *much enlarged: remainder approximately natural size.*)

Fig. 16. Dorsal and ventral views of pedicels of a fatuoid oat. Note large callus residues at the apex of the pedicel and the oblique line of cleavage.

Fig. 17. Callus residues in Type A plants. Note their cleavage surfaces and intermediate character as compared with Figs. 16 and 19.

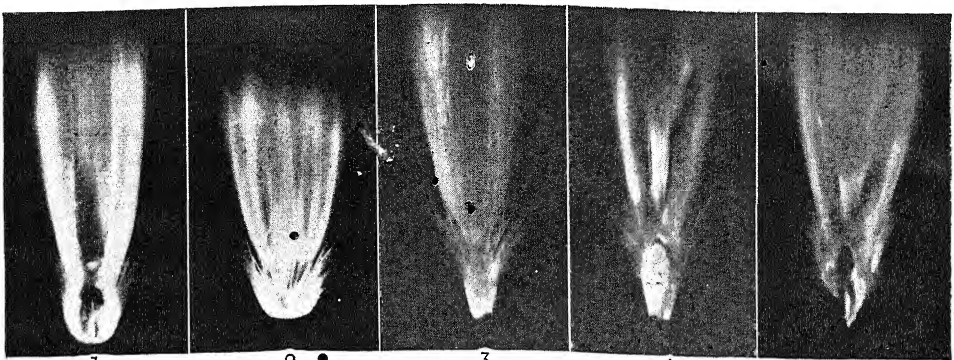
Fig. 18. Callus residues on the pedicels of weakly awned plants *ex* Red Algerian × Scotch Potato. Note similarity to those of Fig. 17.

Fig. 19. Callus residues on pedicels of cultivated or normal (*A. sativa*) plants. Note the very small callus residue and its transverse fracture.

Fig. 20. (*a*) Spikelets and grains of the Type A mutant *ex* Ceirch-du-bach. Note all grains are strongly awned: base of second grain glabrous and solidified as in Ceirch-du-bach normal. (*b*) Spikelets and grains of heterozygous Type A × normal Ceirch-du-bach. (*c*) Spikelets and grains of normal Ceirch-du-bach. (*d*) Spikelets and grains of fatuoid Ceirch-du-bach.

Fig. 21. (*a*) Lower and upper grains of Fulghum (*A. sterilis culta*). Left: fatuoid. Right: normal. (*b*) Spikelets and grains of the sub-fatuoid mutant. Note the awned condition of all the grains and adherence of the florets in the spikelets. (*c*) Spikelets and grains. Left: of the Type B mutant. Right: of the normal or parent strain.

Fig. 22. (*a*) Spikelets and grains of a segregate of Red Rustproof × Scotch Potato, showing weak, non-twisted awns: also basal pubescence of the lower grain. (*b*) Spikelets and grains of Type C, showing very strong, twisted and geniculate awn of the primary and the awnless nature of the secondary grains. (*c*) Spikelets and grains of Type D, showing long, twisted and geniculate awns on all lower grains and on occasional second grains. (*d*) Spikelets and grains of Scotch Potato (*A. sativa*). Left: fatuoid. Right: normal.



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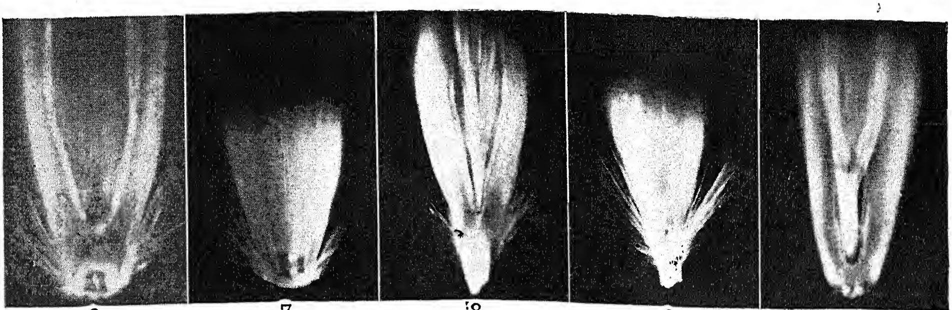

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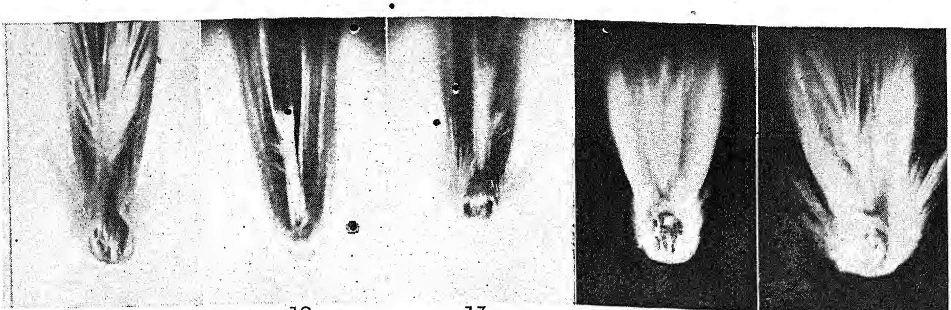

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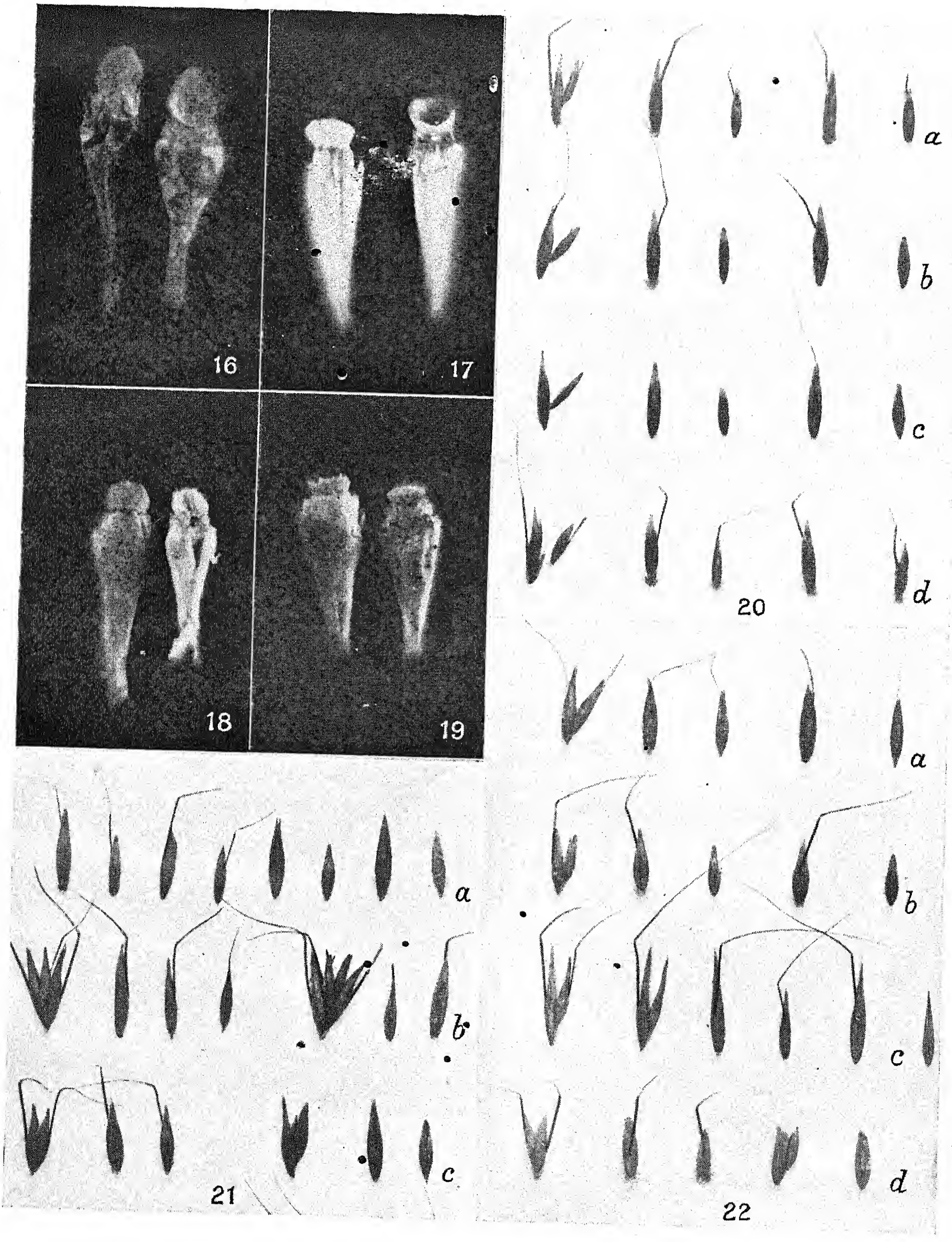
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ON THE OCCURRENCE OF XX MALES IN *LEBISTES*, WITH SOME REMARKS ON AIDA'S SO-CALLED "NON-DISJUNCTIONAL" MALES IN *APLOCHEILUS*.

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I. Introduction.

While, as a general rule, the females of *Lebistes reticulatus* are phenotypically plain greyish, and the males coloured in various ways, the former occasionally develop some colour and on the whole show male characters. In certain cases the anal fin is even transformed into the characteristic male gonopodium. This fact was mentioned in one of my earlier papers on *Lebistes* (1927), and Blacher reported similar observations in 1926. Both Blacher and I observed that the sex glands in such circumstances might contain both ovarian and testicular tissue.

As was to be expected, the coloured females assume the colours according to their genetic constitution, as shown in Figs. 15–17 of my 1927 paper.

Further investigation has revealed several cases of such a partial sex alteration, and it is noteworthy that the male secondary sexual features are especially prone to appear in the females of certain *Lebistes* races, sometimes quite a number of sisters without exception being altered in this way.

As I have formerly (1927) shown, there is nothing to hinder such a partially masculine female from functioning as a female and giving birth to normal offspring.

The fact that this alteration of the females in the male direction was to be observed only in certain *Lebistes* races clearly points to differences in genetical constitution in such races, and hence to the possibility of producing, by suitable crossings, individuals in which the gene combination was of such a kind that the sex alteration becomes total.

As already shown (1922 *a*, *b*, 1923, 1927), *Lebistes* females are homogametic, XX, while the males are heterogametic, containing an X- and a Y-chromosome in the somatic cells. Both X and Y may contain genes for the development of colour patterns; in fact, the Y-chromosome

always carries a disposition to colour, whereas the X-chromosome may be empty. Crossing-over takes place both between the X's in the females and between X and Y in the males, and this last fact proves that the sole real difference between X and Y is that the Y-chromosome contains a dominant male-determining gene, while X contains either a recessive female-determining gene or no specific female gene at all. For, if this were not the case, the difference between X and Y must be gradually blurred by continuous crossing-over, which does not happen, as genetic experiments clearly show.

Hence, in *Lebistes* there must be a single superior, epistatic male gene in the Y-chromosome, decisive for the sex determination; a marked difference from *Drosophila melanogaster*, where the presence or absence of the Y-chromosome is immaterial. Further, my earlier investigations made it likely that a series of allelomorphic male-determining genes occurred in the Y-chromosome of the various *Lebistes* races, the male gene in the different races giving a different colour pattern.

A series of investigations on the topography of the Y-chromosome, especially on the location of the male gene in relation to the rest of the genes, will be published on another occasion. Here we shall deal only with the genotypically conditioned sex shift in the females.

II. Production of XX males.

The females which in my experiments have shown a tendency to alter in the male direction are such as are homo- or hetero-zygous for the genes *Coccineus* + *Vitellinus*[1] in the X-chromosomes, $X_{Co, Vi}\ X_{Co, Vi}$ or $X_O\ X_{Co, Vi}$, also such as possess the genes *Luteus* + *Tigrinus* in X, $X_{Lu, Ti}\ X_{Lu, Ti}$ or $X_O\ X_{Lu, Ti}$, and sometimes also females with the *Elongatus*-gene, *El*.

A cross between a female $X_{Co, Vi}\ X_{Co, Vi}$ and a male $X_{Lu, Ti}\ Y_{Ma}$ produced a very interesting result. "*Ma*" denotes the gene *Maculatus*, which is one of the allelomorphic male genes; this gene has never, even among tens of thousands of individuals, been transmitted to a female. It is firmly attached to the Y-chromosome and is transmitted constantly from father to son, generation after generation, and must be considered as identical with the male gene itself.

[1] As misunderstandings have arisen from my formerly designating all the genes with small letters, in consequence of which they have been wrongly regarded as recessive, I shall here designate them with capital letters to signify more clearly that their effect is visible in a single dose. The recessive alternatives (allelomorphs) are all equal to zero.

The result of the cross mentioned might be expected to take the following course:

$$\begin{array}{cc} ♀\ (\text{No. } 1153) & ♂\ (\text{No. } 1103) \\ X_{Co,\,Vi}\ X_{Co,\,Vi} & X_{Lu,\,Ti}\ Y_{Ma} \\ X_{Co,\,Vi}\ X_{Lu,\,Ti} & X_{Co,\,Vi}\ Y_{Ma} \\ ♀♀ & ♂♂ \end{array}$$

Hence the colour patterns of all the sons (as pictured in the coloured plates of my 1927 paper) would be expected to show the three genes *Coccineus*, *Vitellinus* and *Maculatus*, while the biotype of the females, as is known, cannot be judged from their appearance.

The result was, however, that among 58 sons 55 were of the expected type, while 3, which lacked the *Maculatus* gene, contained *Coccineus*, *Vitellinus*, *Luteus* and *Tigrinus*—viz. the genes that were to be expected in the daughters. As regards sex, these three were completely normal males.

There are two possible explanations. We might suppose crossing-over to have occurred between the X- and the Y- chromosome of the father, so that $Lu + Ti$ had been exchanged with Ma; but this eventuality is excluded by the circumstance that the *Maculatus* gene has never once shown crossing-over among tens of thousands of cases. Hence the appearance of 3 cross-over males among 58 is almost inconceivable. The second possibility is that the three males contained XX and were chromosomally females. This hypothesis is, of course, verifiable, but it is a not unlikely one since both *Co, Vi* and *Lu, Ti* females, as already mentioned, are apt to develop male characters.

The crucial experiment consists in pairing the supposed $X_{Co,\,Vi}\ X_{Lu,\,Ti}$ males with $X_0\,X_0$ females, *i.e.* with females that contain no colour genes in X, and have shown no tendency towards the development of male characters. All the progeny receive two X-chromosomes and should be female, though there is, of course, the possibility that some few of the XX individuals might be totally or partially masculinized anew.

This pairing was made for the three males (see scheme below), and, as was expected, all the progeny were females. The three males produced 101, 140 and 73 daughters, respectively, a total of 314. They were all characteristic females, though a few showed faint indications of colour,

especially in the caudal fin, where the yellow colour conditioned by the gene *Luteus* was faintly visible.

Normal ♀	Homogametic ♂
$X_O \, X_O$	$X_{Co,\,Vi} \, X_{Lu,\,Ti}$
$X_O \, X_{Co,\,Vi}$	$X_O \, X_{Lu,\,Ti}$
♀♀	♀♀

Considering that my experiments with *Lebistes*, which cover a long series of years, have never before given a progeny of females only, the proportion being generally about 1 : 1 (in several species of Poeliciides there is a surplus of females; cf. Geiser, 1924), this result must be considered a valid proof that the three males mentioned have a XX chromosome set, and thus are homogametic.

Again, half of the daughters of the XX males must contain X_O $X_{Co,\,Vi}$ and the rest $X_O \, X_{Lu,\,Ti}$; this cannot be ascertained directly, but the five females taken out at random for a test corresponded to this expectation. By crossing them with $X_O \, Y_{Ma}$ males, one proved to belong to the former type and four to the latter.

By back-crossing the XX males with their own daughters, so far only females were produced, 107 altogether, several of which, however, showed male characters. No completely male individual has hitherto been observed.

III. The quantitative nature of the sex difference.

The possibility of producing XX males in *Lebistes* is interesting in several ways. It shows that not only the Y-chromosome contains a male-determining gene, but that also the X-chromosomes themselves contain genes influencing the sex determination. In certain races, however, this influence may be only faintly female, or it may be as much male as female, or else it may even appear as a male-determining tendency. The theory that the difference between male and female is not of a qualitative but of a quantitative nature, as developed more especially by Goldschmidt and Witchi, receives strong support from these facts.

Thus the possibility drops, which I had not formerly dared to exclude, that the male-determining gene in the Y-chromosome in *Lebistes* was in

the main restrictive of the female sex, and that there were no specifically sex-determining genes in the X-chromosome. The experiment proves the presence in the X-chromosome of one or more sex-determining genes of a now more female, now more male nature, whereas it is not proved that the male gene of the Y-chromosome has an allelomorph in the X-chromosome.

What has further been made clear in this experiment is the fact that the autosomes, as I have also formerly presumed (*l.c.* 1927), contain sex-determining genes, for this alone will explain the circumstance that only 3 out of the 58 XX animals were males. $X_{Co,\,Vi}\,X_{Lu,\,Ti}$ is not in itself sufficient to bring about male sex. Only about one-sixteenth of the individuals of this formula developed into males, which may be considered a proof of a sex-determining co-operation of autosomal sex genes. To conclude from the evidence that about one-sixteenth of the XX animals were males, that just two recessive autosomal sex genes had a share in the sex determination, is, however, hardly permissible.

The case is especially interesting in that the Teleosteans are so far the only example of the fact that within closely related organisms the male sex is heterogametic in certain types (*Lebistes*—Winge, *Aplocheilus*—Aida) and the female sex in others (*Platypoecilus*—Gordon, Fraser). Since it is possible to produce homogametic males in *Lebistes*, the question arises whether it is possible to find or to produce heterogametic females. It is no doubt exclusively a question of the strength of the respective male or female dispositions, whether the male or the female is heterogametic. Schematically expressed, it may be said that if the genes of the X-chromosome with a female tendency are stronger than the genes of the Y-chromosome with a male tendency, then female heterogamety is possible; whereas, if the masculine tendency of the Y-chromosome is stronger than the feminine tendency of the X-chromosome, the male heterogamety is possible. As to the homogametic sex, the experiment clearly shows that it is possible by a proper selection to produce both homogametic males and females that are able to function normally. In all circumstances it is obvious that the difference between the two types of heterogamety, generally regarded as essential, may not be significant.

IV. SOME REMARKS ON AIDA'S SO-CALLED "NON-DISJUNCTIONAL" MALES IN *APLOCHEILUS*.

In a paper on his further studies of *Aplocheilus* (1930) Aida gives an account of some interesting results, which he tries to explain on the

supposition of non-disjunction. There are, however, as yet no cytological investigations in support of this hypothesis, and I feel convinced that Aida's results have nothing to do with non-disjunction, but are to be explained in the same way as the aberrant males in *Lebistes* discussed above.

Aida crossed heterozygous red *Aplocheilus* males $X_R\,Y_r$ with white females $X_r X_r$, and, as was to be expected, found red daughters and white sons. But among some 5000 individuals appeared 5 white daughters and 9 red sons. Only the exceptional sons were fit for a closer analysis, and, in the case of two, proved to be due to crossing-over in the father, through which $X_r\,Y_R$ sons were produced. The remaining 7 exceptional sons were regarded as non-disjunction males of the formula $X_R X_r Y_r$, it being presumed that both X_R and Y_r had entered with the spermatozoon. These males, crossed with white females of the formula $X_r X_r$, gave almost exclusively females, viz. 996 red and 953 white, and only 19 males, of which 11 were red and 8 white.

In this connection Aida says (*l.c.* p. 5): "The production of the red and white females makes it necessary to consider that the male parent had two X's, an X_R and an X_r. The genetic formula having a double dose of X is characteristic of females, but as these individuals are male, not female, they must necessarily have some male-determining factor which is more powerful than two X's. The phenomenon may be explained fairly well by the supposition that all these exceptional red males are the result of non-disjunction between sex chromosomes and have a Y-chromosome in addition to two X's."

If we compare the circumstances in *Lebistes* described above with those observed by Aida in *Aplocheilus*, it is evident that we are dealing with the same phenomenon; but Aida had not at his disposal a sufficient number of genes in the chromosomes concerned to determine which chromosomes entered into the exceptional males. To judge from *Lebistes*, Aida's exceptional males are $X_R\,X_r$ males, *i.e.* individuals that in spite of their XX constitution have developed in the male direction in consequence of a casual accumulation, in the X-chromosomes and in the autosomes, of genes with a faintly female and stronger male effect respectively. Normal sex determination, depending on XX or XY constitution, is here disturbed, other genes having taken the lead in the sex determination.

Aida's view of non-disjunction also presents other difficulties. Since the progeny of the exceptional males are almost all females, he has to suppose that it is always the two X-chromosomes which conjugate

previous to the reduction division, Y remaining isolated, and that "the superfluous solitary Y-chromosome lagging in the middle of the spindle might be excluded from the formation of the gametic nuclei" (*l.c.* p. 13). "In *Aplocheilus*, indeed, the frequency of the occurrence of heterosynapsis in non-disjunctional males may be well conceived roughly to be zero" (*l.c.* p. 14). Aida is evidently disturbed by the presence of a Y-chromosome.

The very few sons which these exceptional males produce are again "non-disjunctional," *i.e.* they, too, produce almost all daughters; although we find an increasing number of sons as the generations progress. "What caused this increase—whether the presence of some gene or some local external condition—is not known at present" (*l.c.* p. 13). Though inexplicable on non-disjunction, this increase is easily understood on the supposition that the exceptional males have the XX formula; for males of this formula must normally produce only daughters, but may give rise to a few sons when accidental circumstances, or inbreeding in certain individuals, cause an accumulation of the genes with a male tendency (*i.e.* in the autosomes). Inbreeding will theoretically explain why the number of males increases generation after generation, but it cannot be seen from Aida's tables whether inbreeding has taken place, or no.

The strangest phenomenon in Aida's material is the red male N which was produced as the only son by the crossing of a supposed non-disjunctional male with a white female; this male was the only brother of 125 red females and 91 white females. The progeny of the male N consisted of 133 females and 156 males, which suggests that it behaves as a normal male. Its sons, too, behaved as normal XY males. Aida considers this male a proof that the father must actually have contained a Y-chromosome ($X_R X_r Y_r$). Even if mistakes in the experiments are left out of account here, it seems more likely to me that we have here a case in which a great accumulation of male-determining genes has taken place (through crossing-over) in one of the X-chromosomes of an XX male, so that the equivalent of a new Y-chromosome may be said to have arisen, which for the future takes the lead in the sex determination.

Altogether, it may then be said that, as the experiments on *Lebistes* clearly show that XX males may arise, and that these, like Aida's exceptional males, produce practically only daughters, there is every reason to regard the *Aplocheilus* males in question as being of the same nature. Cytological investigation might decide the question.

SUMMARY.

In certain *Lebistes* races the females (XX) are apt to show male characters and develop colour, though normally only males (XY) show colour patterns. By appropriate crossings of such races it proved possible to produce a few XX males. Such males mated with normal females gave only females; through inbreeding it is possible to produce individuals again which are more or less altered in a male direction.

These experiments show that, although genes in the X-Y-chromosome pair normally are alone decisive as regards sex, it is possible through selection to produce types in which other chromosomes take over the sex determination. They show also that both X-chromosomes and autosomes contain genes which have a share in the sex determination.

The remarkable fact that the closely related *Platypoecilus* has homogametic males and heterogametic females is explained on the ground that the sex determination is of a quantitative nature, so that the heterogamety may change from being a male to being a female characteristic.

Aida's so-called non-disjunctional males in *Aplocheilus* (1930), which in like manner produce nearly all females, must be regarded, not as having arisen through non-disjunction, in which case they should contain XXY, but as being XX males.

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NOTE ON A TRI-COLOUR (MOSAIC) MOUSE.

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THE occurrence of rats and mice having skin areas of two different colours in addition to white is sufficiently uncommon to deserve record. In the following note I have endeavoured to put together all information likely to be useful to other workers, on a case which occurred in my stock during the spring of 1929.

A pair of litter-mates, born 23 February, 1928, were mated to carry on a stock line segregating in the two factors: **Bb**, black *v.* chocolate, and **Ww**, white *v.* recessive pied. Of their eleven litters one was lost by incursions of wild mice, and the young recorded from the remainder are shown below in Table I.

TABLE I.

	Pied		White		
	Black	Chocolate	Black	Chocolate	Uncertain
♀	5	7	7	2	0
♂	7	4	1	11	2
Total	12	11	8	13	2

In the eleventh litter, born 5 February, 1929, occurred the exceptional doe, classified above as a black white, having small black patches on either side of the rump and a distinct chocolate dot between the right eye and ear. The eyes, which, in certain lights, appear distinctly brown in chocolate mice, have always appeared to be both black, and since the chocolate spot is close to the right eye it is probable that the area affected is small. It will be noticed that the parents were at the time near the end of their reproductive period, being nearly a year old.

No comparable case has hitherto occurred in this stock out of some 7000 mice bred in the last few years, of which about 1500 were heterozygous, **Bb**, and the effect not masked by dilution.

In mating her it was desirable in the first place to test if she were genetically **bb** or **Bb**, which could best be done by back-crossing to chocolate; in the second place, to test the possibility that the condition was favoured by her particular genetic constitution by mating to one of her own sons, and thirdly, in view of the possibility that chocolate areas

are more readily formed on the edge between black and white areas, to make sure that such boundaries were available over as much of the body as possible, as in the whiter strains of dominant pied. Her first litter was therefore from a chocolate buck, **bbWwSs**, from such a strain, and consisted of two self does, black and chocolate respectively, three pied bucks, two blacks and one chocolate, and three white bucks, one of which was certainly chocolate. The chocolate pied buck was certainly dominant pied, **WwSs**, but either or both of the black pied males may have been recessive pied **wwss**, since the cross was segregating heavily for modifiers and they were not subsequently tested.

For further matings the chocolate dominant pied son has been used and nine further litters obtained. These are shown in Table II.

TABLE II.

	Black				
	Self	Dominant pied	Recessive pied	White	Total
♀	1	5	2	2	10
♂	0	4	0	2	6
Total	1	9	2	4	16

	Chocolate				
	Self	Dominant pied	Recessive pied	White	Total
♀	2	6	3	4	15
♂	0	6	2	7	15
Total	2	12	5	11	30

All the whites could be classified by skin spots except one black male and one brown female, which were classified by the eyes. There were thus fifteen blacks which might have, but did not show tri-colour spotting. This is sufficient to exclude any hypothesis which requires that half the young should be tri-colour, but not to exclude a quarter or smaller fractions. It may be inferred either that the tri-colour coat is not genetically conditioned, or that it frequently fails to appear in mice of suitable genetic constitution. On the former view the present case may reasonably be regarded as a mosaic from part of whose body the **B** gene has been lost during cell division.

It will be noticed that in the second mating there is an excess of chocolate young. Taking the two matings together, there are thirty-three chocolate to nineteen black, an excess which, while scarcely differing significantly from the 1 to 1 expectation, lends some colour to the

suggestion that the black gene may have been lost also from some part of her germinal tissue, as in the case of the mosaic guinea-pig reported by Wright and Eaton.

DISCUSSION.

The closest parallel with the tri-colour here described is provided by three individuals reported by Pincus (1) in February 1929. His cases concern not only the same species, but the same factor, and consist of three pied mice showing both black and chocolate areas. I presume from Pincus' description that all were recessive pied, being in this unlike the doe here reported. Pincus describes all three as genetically heterozygous, **Bb**, but in the case of his doe the evidence consists only of a single litter by a black brother, yielding two black and one chocolate. She may therefore have been homozygous chocolate in the germinal tissue. The two bucks were tested extensively by mating to chocolate and both of these gave a slight but apparently insignificant excess of blacks, none of which were tri-colour. In both of these the chocolate area was on the back, and Pincus emphasises the fact that this area is in other mice of the same stock often occupied by white spotting. This leads him to suggest an alternative to the view that the **B** gene has been lost by somatic non-disjunction, namely that in the border areas which in mice of the same strain are sometimes pigmented, sometimes white, and which may be designated "critical for pigmentation," a recessive gene may exercise a controlling effect. This view is supported by the fact that the chocolate areas in the two bucks, though of different sizes, were in the same place. The two bucks were not, however, nearly related and the tri-colour character did not appear in about 150 black offspring. It is not stated that the mates were chosen from near relatives of the tri-colours.

An extremely interesting case in rabbits was reported at the same time by Castle (2), involving the dilution factor, which changes black to blue. A buck, which was subsequently shown to be heterozygous in this factor, had a large blue spot on the left shoulder extending to the white areas on the foot and neck. With blue does he produced forty-one blue, forty-four black and two tri-colours, black Dutch with areas of blue, though smaller than those on the father. In one case the patch was on the forehead where a Dutch rabbit would normally show white, and in the other it was a transverse belt on the right side, from the mid-ventral line adjacent to the white belt to the middle of the back.

The original tri-colour when mated with yellow, for which he was also heterozygous, produced one tri-colour out of eleven not-yellow offspring, this being a black Dutch doe having a blue spot in the position of the

usual white blaze. Mated to his mother who was homozygous black, he had, besides yellow offspring, twenty-two black ones, none of which were tri-colour. No tri-colours again were produced from his heterozygous sisters and daughters, one of whom was herself a tri-colour. Castle concludes that he "transmitted the tri-colour condition in a small percentage only of his gametes, which we can estimate at 3 or 4 per cent. of his intensity-transmitting gametes." The absence of tri-colours among the six black young by his tri-coloured daughter does not, however, support the view that the difference between his black and his tri-colour offspring was wholly gametic. That it is partially so is suggested by the record of one of his tri-colour sons, who by blue females has produced sixty-six blacks, seventy-one blues and three tri-colours. In his case also mating with his tri-colour sister has produced no tri-colours, there being five blacks each of which has a two-thirds probability of being heterozygous.

There can be little doubt in this case that the tri-colour condition is determined, at least in part, genetically, and its low incidence among the heterozygous offspring shows how easily its genetic nature might escape observation in cases in which few offspring can be produced.

A well-established example of a non-transmitted mosaic was reported by Wright and Eaton in 1926 (3). This was a buck guinea-pig who was apparently a mutant from albino dilution, $\mathbf{c^d}$, to the wild type, **C**. His coat showed both $\mathbf{c^d}$ and **C**, and as he lived to sire 228 young it was possible to establish two important facts, (i) that he failed to transmit the mosaic appearance to any of the seventy-nine offspring which received **C** (intense coloration), and (ii) that he must have been a mosaic in the germinal tissue, since much more than half of his offspring were dilute. Wright and Eaton suggest that his germinal epithelium was 70 per cent. heterozygous and 30 per cent. homozygous dilute. In spite of some appearance to the contrary, the proportion of the two kinds of offspring does not seem to have varied significantly during his lifetime.

With the exception of Castle's case there is no reason to go beyond the hypothesis that we are dealing with simple mosaics caused by the loss of a greater or smaller fragment of chromatin; on the other hand this one example, where the peculiarity was unquestionably inherited, must make us hesitate in other cases also to assume that the genetic constitution has not influenced the "mosaic" appearance. A somewhat lower incidence among the offspring than that observed by Castle would have escaped observation even in the large progenies obtained by Pincus and by Wright and Eaton, especially if inbreeding were not practised. In the case of the guinea-pig, the view that we have to do with a somatic mosaic is

strongly supported by the anomalous frequency ratio of the offspring, and the same is true in less degree of the mouse here reported. The association with white areas in Pincus' mice, as in Castle's rabbits, is, however, suggestive of the view that in certain exceptional genetic combinations an abnormal pigmentation in these areas may be induced without non-disjunction. Finally, it is not impossible that the frequency of somatic non-disjunction may itself be influenced by the genetic composition.

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(1) Pincus, G. (1929). "A mosaic (black brown) coat pattern in the mouse." *Journ. Exp. Zool.* LII, 439–41.

(2) Castle, W. E. (1929). "A mosaic (intense dilute) coat pattern in the rabbit." *Ibid.* LII, 471–80.

(3) Wright, S. and Eaton, O. N. (1926). "Mutational mosaic coat patterns in the guinea-pig." *Genetics*, XI, 333–51.

THE HISTORY OF A TETRAPLOID SAXIFRAGE.

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(With Four Plates and Two Text-figures.)

The genus *Saxifraga* is one of the large genera of flowering plants. In the latest systematic monograph[1] 302 species are described, but most systematists would increase this number considerably, since many of the subspecies of this work are usually accepted as species. The genus reaches its greatest development in the North Temperate, Arctic, and Subarctic zones, and includes 25 accepted British species[2], though it is doubtful if all of these are valid species.

The species with which we are now concerned are *S. rosacea* Moench (*S. decipiens* Ehrh.) and *S. granulata* L. The former is reduced by Engler and Irmscher to a subspecies of their "typus polymorphus" *S. caespitosa*, as subsp. *decipiens* Engler et Irmsch. It is, however, retained as a species by most British authors and is so considered here, mainly for convenience since its exact taxonomic status is of little immediate importance. It is placed in the Section *Dactyloides* Grex *Caespitosae*, and has a wide distribution in the mountains of Western and Central Europe. *S. granulata* is another "typus polymorphus" of Engler and Irmscher, but is placed by them in the Section *Nephrophyllum* Grex *Granulatae.* In the stricter sense (*i.e.* as the subsp. *eugranulata*) it also has a wide distribution, through Central, Western, and Southern Europe, more especially in the hills and mountains, and, at lower altitudes, occurs in Scandinavia and North Russia. The character of the Section *Nephrophyllum* is the production of bulbils or gemmae as hibernating (or aestivating) organs. Contrasted with this character the species of the Section *Dactyloides* produce offsets or branches of some kind, usually with a rosette of leaves remaining green throughout the year, and always having a distinctly elongated axis. The above sectional characters appear to have considerable taxonomic value and, in general, to bring together species most alike in the total of their characteristics. We emphasise this because we are here concerned with the results obtained by the crossing of two species not accepted as of close alliance within their genus.

[1] Engler und Irmscher, *Pflanzenreich*, IV, 117, I–II (1916–19).
[2] Druce, *British Plant List*, 2nd ed. 1928.

Several records of crosses between *S. rosacea* (*S. decipiens*) and *S. granulata* have been published. We have traced the following: *Verh. zool.-bot. Ges. Wien*, XIX, 556 (1869); *Delectus seminum horti Vratislaviensis*, 1869; *Bot. Zeit.* XXX, 548 (1872); *Gartenflora*, XXXV, 306 (1886); Focke, *Die Pflanzen-Mischlinge*, 148 (1881). None of these records is of primary importance.

Our attention was called to the desirability of investigating the genetical relationships of these species by the occurrence of a chance cross in the Orders' Beds at Potterne, Devizes, where both plants grow close together[1]. *S. granulata* also crossed naturally with *S. caespitosa* L. and *S. drucei* E. S. Marshall.

The material used for the controlled hybridisation was obtained from the following sources: *S. rosacea*, from Western Ireland, communicated by F. J. Hanbury; *S. granulata*, a grassy habitat at Coulston, Wilts. Selfing tests showed that both the original stocks bred true.

In the cross, the characters of whose offspring are recorded in this paper, *S. rosacea* was used as the female parent and *S. granulata* as the male. This is of interest because on the whole the *S. granulata* characters are more obvious in the F_1 and subsequent generations than are the specific characters of *S. rosacea*.

PARENTS AND F_1 GENERATION.

The following table gives the characters of the two parents and of the F_1 offspring.

S. rosacea	*S. rosacea* ♀ × *S. granulata* ♂ F_1 (Plants B 2)	*S. granulata*
Habit. The central rosette ends in an inflorescence and from the axils of its leaves there arise three to twelve sterile rosettes, compacted round the base or slightly elongating but with a distinct axis, 1·5 to 4 cm. long. Plants average 12 cm. high.	*Habit.* The rosettes with flowering stems as in *S. granulata*. Bulbils occur in the axils of the lowermost leaves, but some at least grow out immediately into short rosettes. Plants average 23 cm. high.	*Habit.* A flowering stem arises from the centre of each rosette and has no sterile rosettes at its base. Numerous bulbils arise at the base of the flowering stem in the axils of the lowermost leaves at soil level and even on rhizomes below the soil in the axils of scale leaves. Plants average 25 cm. high.
Rosette leaves ovate—spathulate in general outline, usually three-lobed but sometimes one or two of the lobes with an extra smaller lateral lobe, 9–14 mm. long, at the base 2·5 to 3 mm. broad, across the lobes 5 to	*Rosette leaves* with distinct lamina, petiole, and base; lamina oblate, cordate-reniform at base, the number, size and depth of the lobes or crenulations vary, with a hydathode near the apex of each but	*Rosette leaves* with distinct lamina, petiole, and base; lamina oblate, cordate at base, the number, size and depth of the lobes or crenulations vary, with a hydathode near the apex of each but no apical hairs,

[1] See *Journ. R. Hort. Soc.* LI, p. xxxv (1927).

S. rosacea	*S. rosacea* ♀ × *S. granulata* ♂ F_1 (Plants B 2)	*S. granulata*
10 mm. broad, lobes oblong to narrow elliptic-oblong acute, 3 to 4 mm. long, 1·5–2 cm. broad, long hairs from the margin in the lower part and from the margin and upper surface of the lobes, no glands, hydathode immediately below the apex on the upper surface of each lobe and usually a long hair at each apex; part below lobes ("petiole") up to 8 mm. long.	no apical hairs, average size 18·5 mm. long, 21 mm. broad, with long white distinct hairs on both surfaces mixed with a few glands; petiole 37 mm. long, with spreading white hairs; base 13 mm. long and 3 mm. broad, with very long white hairs.	average size 14 mm. long, 16 mm. broad, with rather long white distinct hairs on both surfaces mixed with a few glands; petiole 14 mm. long, with spreading white hairs; base 8 mm. long and 5 mm. broad, with long and dense white hairs.
Flowering stem erect, terete, purplish red, with few long non-glandular white hairs and a medium number of shorter glandular red-tipped hairs.	*Flowering stem* erect, terete, purplish red or greenish, with dense long white non-glandular hairs below and with dense short glandular red-tipped hairs above.	*Flowering stem* erect, terete, purplish red, with dense long white non-glandular hairs below and with dense short glandular red-tipped hairs above.
Stem leaves showing a gradual transition and simplification from rosette leaves to bracts, more deeply lobed than rosette leaves and in upper ones only one to two lobes, hairs are present on both surfaces and some are glandular.	*Stem leaves* showing a gradual transition and simplification from rosette leaves to bracts, more deeply lobed than rosette leaves and in upper ones only one to two lobes, as traced upwards they gradually become more glandular on both surfaces.	*Stem leaves* showing a gradual transition and simplification from rosette leaves to bracts, more deeply lobed than rosette leaves, and in upper ones only one to two lobes, as traced upwards they gradually become more glandular on both surfaces.
Inflorescence branches much more densely glandular than the stems. Each stem four- to five-flowered.	*Inflorescence branches* as the top part of the stems, *i.e.* very densely glandular. Each stem up to forty-flowered.	*Inflorescence branches* as the top part of the stem, *i.e.* very densely glandular. Each stem up to twelve-flowered.
Calyx and receptacle densely glandular with short red-tipped hairs, sepals ovate sub-obtuse to rounded, 2·5 mm. long, 2 mm. broad, enlarging to 3 mm. by 2·5 mm. in young fruit.	*Calyx* and receptacle densely glandular with short red-tipped hairs, sepals oblong-ovate sub-obtuse, 3 mm. long, 2·5 mm. broad, enlarging to 3·5 mm. by 3 mm. in young fruit.	*Calyx* and receptacle densely glandular with short red-tipped hairs, sepals lanceolate-oblong, acute, 4 mm. long, 1·5 mm. broad, enlarging to 4·5 mm. by 2·5 mm. in young fruit.
Corolla: 14 mm. diam.; petals obovate, 7·5 mm. long, 5–6 mm. broad, apex rounded, truncate at base, three green veins distinct from just above base to half the length of the petal, quite indistinct above (by reflected light), sometimes one or two faint lateral nerves added.	*Corolla:* 19 mm. diam.; petals obovate, up to 13·5 mm. long and 8·5 mm. broad, apex rounded, slightly narrow truncate at base, five to eight green veins, the middle ones running up distinctly three-quarters the length of the petal.	*Corolla:* 20 mm. diam.; petals oblanceolate, up to 16 mm. long, 5 mm. broad, apex rounded to obtuse, slightly narrowed at base, five green veins, the three middle ones running up distinctly three-quarters the length of the petal.
Androecium: greenish yellow, becoming pink with age, glabrous; filaments up to 4 mm. long.	*Androecium:* greenish yellow, becoming duller and red-tinged with age, glabrous; filaments up to 5·5 mm. long.	*Androecium:* greenish yellow, becoming duller and red-tinged with age, glabrous; filaments up to 6·5 mm. long.

S. rosacea	*S. rosacea* ♀ × *S. granulata* ♂ F_1 (Plants B 2)	*S. granulata*
Gynaeceum with the two styles quite distinct, 2·5 mm. long (including stigma), at first parallel, later diverging; stigmas obliquely capitate; ovary apex level with receptacle.	*Gynaeceum* with the two styles quite distinct, 4 mm. long (including stigma), at first parallel, later diverging; stigmas markedly oblique; ovary projecting 0·75 mm. above the receptacle.	*Gynaeceum* with the two styles quite distinct, 5 mm. long (including stigma), at first parallel, later somewhat diverging; stigmas markedly oblique; ovary projecting 1 mm. above the receptacle.
Fruits relatively short and broad, projecting 4·5 mm. beyond the receptacle (including the persistent styles), 4 mm. diam.	*Fruits* relatively short and broad, projecting 5 to 6 mm. beyond the receptacle (including the persistent styles), 4 to 5 mm. diam.	*Fruits* relatively longer and narrower, projecting 6 mm. beyond the receptacle (including the persistent styles), 2·5 mm. diam.
Seeds brownish black, ovoid-cylindric, 0·75 mm. long, papillose.	*Seeds* brownish black, ovoid-cylindric, 0·75 mm. long, papillose.	*Seeds* brownish black, ovoid-cylindric, 0·5 mm. long, papillose.
Post-fruiting habit evergreen.	*Post-fruiting habit.* The plant is never completely bare of green leaves, since new shoots appear as the old leaves die off.	*Post-fruiting habit.* The aerial parts die right down after fruiting and new green shoots begin to appear about the middle of August.

The figures given for seed lengths in the above table are averages. Fluctuations in length occur in pure-bred seeds of both parents as well as in the F_1 and subsequent generations.

The F_1 generation consisted of 26 plants which were morphologically uniform for the above characters, except for minor individual fluctuations and the presence of petals showing stages towards a tubular structure and poor stamens in one plant. This last was not the plant which was bred from to produce the F_2, since when it was selfed under control it was sterile, though some exposed flowers set a few seeds. Three F_1 plants were selfed under control but only one (B 2 F_1 plant 1) set seed and is the origin of the F_2 and subsequent generations described below. The two self-sterile plants were designated B 2 F_1 plant 3 and B 2 F_1 plant 8.

F_2 GENERATION.

The F_2 generation consisted of 436 individuals. This large generation was remarkably uniform, except for petal abnormalities, and the plants showed no signs of segregation towards the distinct habits of the parents.

Saxifraga potternensis = F_2 from the cross *S. rosacea* ♀ × *S. granulata* ♂.

Habit. The rosettes have flowering stems as in *S. granulata*, and bulbils are present in the axils of the lowermost leaves at soil level. The plants average 26 cm. high. New shoots appear as the old leaves die off or even before.

Rosette leaves with distinct lamina, petiole, and base; lamina oblate,

cordate-reniform at base, the number, size, and depth of the lobes or crenulations vary, with a hydathode near the apex of each but no apical hairs; the size varies much, of a medium-large basal leaf 25 mm. long and 33 mm. broad, with long white distinct hairs on both surfaces and few to many gland-tipped ones; petiole 37 mm. long and 3 mm. broad with long white hairs.

Flowering stems erect, terete, purplish red or greenish, with dense long white non-glandular hairs below, and short dense glandular red-tipped ones above.

Stem leaves as in F_1.

Inflorescence branches as in F_1.

Calyx and receptacle densely glandular, with short red-tipped hairs; sepals oblong-ovate, sub-obtuse, 4 to 4·5 mm. long, 2·5 to 3 mm. broad, enlarging to 5 mm. by 3 mm. in young fruit.

Corolla: 19 mm. diam.; petals obovate, 13·5 mm. long, 8·5 mm. broad; apex rounded, slightly narrow-truncate at the base, with five to seven green veins of which the middle ones run up distinctly at least three-quarters the petal length. Twelve plants showed somewhat narrower petals but not so narrow as in *S. granulata.* One plant had some flowers with full broad petals and some with somewhat narrower. Sixteen plants produced flowers, some of which had from one to all of the petals lobed and five aberrant plants had deformed (staminodal) petals. One of the plants which formerly produced some lobed petals, later produced staminodal petals.

Androecium: greenish yellow, becoming duller and red-tinged with age, glabrous; filaments up to 6 mm. long.

Gynaeceum with the two styles quite distinct, 4 mm. long (including stigma), at first parallel, later diverging; stigmas markedly oblique; ovary projecting 1·5 mm. above the receptacle.

Fruits relatively short and broad, projecting 6 to 8 mm. beyond the receptacle (including the persistent styles), 6 mm. diam.

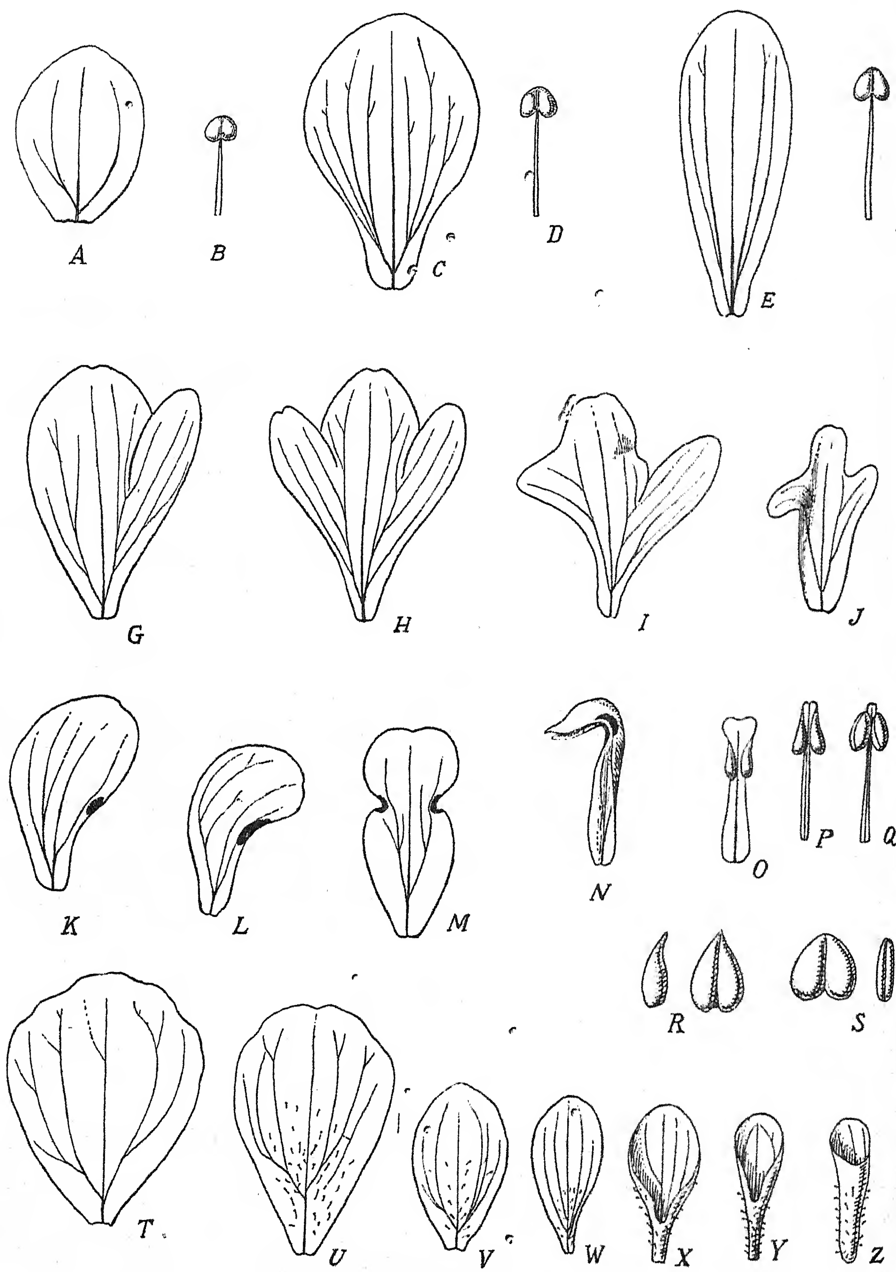
Seeds as in F_1.

F_3 GENERATION.

F_2 plant 1 (*selfed*): 112 offspring, uniform, except that 21 plants had staminodal petals.

F_2 plant 2 (*selfed*): 42 offspring, uniform, except that 5 plants had staminodal petals.

F_2 plant 3 (*selfed*): 107 offspring, uniform, except that 4 plants had staminodal petals.



Text-fig. 1.

F_2 plant 4 (*selfed*): 84 offspring, uniform, no plants with deformed petals.

F_2 plant 5 (*selfed*): 97 offspring, uniform, except that 5 plants had staminodal petals.

F_2 plant 6 (*selfed*): 69 offspring, uniform, except that 8 plants had only normal petals and 61 plants staminodal petals. The parent of this generation is the plant referred to below as having staminodal petals on three branches. That the large majority of plants produced staminodal petals suggests that this character has some kind of genetical basis.

The F_3 plants (511 in number) from the six selfings recorded above are extremely uniform, except for petal characters, and similar to F_2 plants. In other words *S. potternensis* is self-fertile and breeds true on selfing, except for the occurrence of staminodal petals. The non-segregation of parental characters in F_2 and F_3 suggested to us that *S. potternensis* might be tetraploid. A suggestion confirmed by Whyte's researches.

PETAL DEFORMITIES.

Tubular petals. In the F_1 generation one plant (B 2 F_1 plant 3) showed petals in stages of metamorphosis to tubular organs. They are often in

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A. Petal of *Saxifraga rosacea.* (× 3.)
B. Stamen of *S. rosacea.* (× 3.)
C. Petal of F_1 (first-year plant). (× 3.)
D. Stamen of F_1 (first-year plant). (× 3.)
E. Petal of *S. granulata.* (× 3.)
F. Stamen of *S. granulata.* (× 3.)
G. Lobed petal from F_2 plant. (× 3.)
H. Lobed petal from F_2 plant (from the same flower as *G*). (× 3.)
I. Lobed petal from F_2 plant (from another flower of the same plant as *G*). (× 3.)
J. Lobed petal (from the same flower as *I*). (× 3.)
K. Staminodal petal from F_2 plant (No. 2) showing trace of sporogenous tissue. (× 3.)
L. Staminodal petal (from the same flower as *K*). (× 3.)
M. Staminodal petal showing two masses of sporogenous tissue (from another flower). (× 3.)
N. Staminodal petal showing two masses of sporogenous tissue (side view, from another flower). (× 3.)
O. Staminodal petal (from another flower). (× 3.)
P. Staminodal petal (from another flower). (× 3.)
Q. Staminodal petal (from same flower as *P*), showing uncommon dehiscence. (× 3.) In stages *P* and *Q* the anthers fall from the filaments after maturity.
R. Very young anther from stamen in position of a metamorphosed petal, adaxial and lateral views. (× 6.)
S. Very young anther from normal stamen of the first staminal whorl, adaxial and lateral views. (× 6.)
T. Petal from B 2 F_1 plant 3. One of the least metamorphosed petals, only distinguishable from a normal petal by its thicker texture and slightly undulating margins. (× 3.)
U. Petal from another flower of B 2 F_1 plant 3. Glandular hairs on the adaxial surface. (× 3.)
V., *W.* More petals from B 2 F_1 plant 3. (× 3.)
X., *Y.* More or less tubular petals from B 2 F_1 plant 3; adaxial surface showing invagination. (× 3.)
Z. Tubular petal from B 2 F_1 plant 3 (from same flower as *W*). (× 3.)

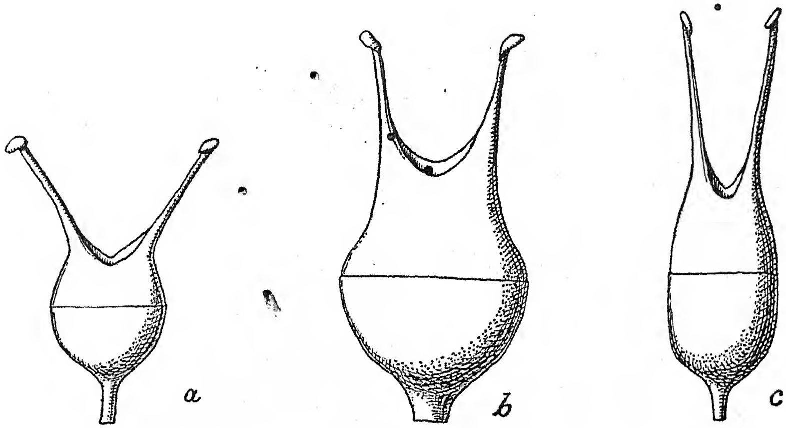
reduced size, have a thicker texture, and glandular hairs on the abaxial surface. In the more extreme examples the margins are turned in adaxially, and in a few there is definite invagination and the formation of a tube recalling the honey glands of *Eranthis* and *Helleborus*. The stamens are often reduced in size, and apparently do not always contain viable pollen, but the normal number (10) is usually present. Occasionally only one carpel is developed in a flower. Even when two carpels mature to the fruit stage the capsule has a shape different from that of the capsules of its sibs, its parents, and plants of F_2 and F_3 derived from a sib. The ripe capsule projects 5 mm. beyond the receptacle and is 3·5 to 4 mm. in diameter. On selfing the plant proved sterile, though on crossing an F_3 plant with pollen from this individual a fair amount of viable seed was obtained. This seed has germinated, but the plants are at present only in the seedling stage. Similarly modified petals have not appeared in any other of the saxifrage plants with which we have worked.

Lobed petals. In certain F_2 plants some of the petals of individual flowers have two or three lobes, the one or two smaller lateral lobes overlapping adaxially the larger middle one. No trace of sporogenous tissue has been detected on these ordinary lobed petals.

Staminodal petals. In much more abnormal flowers in F_2 and F_3 plants various transitions from petals to stamens have been detected. These form an interesting series. In the least staminodal petals (*K* and *L* of Text-fig. 1) the outline is unsymmetrical and a small patch of rudimentary sporogenous tissue shows on the side to which the organ is bent over. In the next stages (*M* and *N*) sporogenous tissue is still more developed, and appears on both sides while the organ is symmetrical about a longitudinal axis. A progressive reduction in size of the whole organ results from reduction in size of the petaloid tissues, and is accompanied by a simplification of the venation. Further reduction in petaloid tissue and increase in sporogenous areas results in the formation of stamens producing apparently viable pollen (*O*, *P*, *Q*, *R*). The enlarged portion above the connective is progressively reduced with increase of sporogenous tissue. Even in the most stamen-like of these metamorphosed petals the anther part can be distinguished from the anthers of normal stamens by the acute connective, the pollen sacs being solitary in each lobe, and usually by the absence of a marked line of dehiscence. Of course, the metamorphosed petals can always be recognised by their position relative to the sepals and two whorls of normal stamens.

The individual F_2 plant 6 calls for some comment. This plant had one branch (bearing 13 flowers) with staminodal petals, two branches with

flowers varying from those with all normal to those with all staminodal petals, and ten branches with all the flowers normal. The condition of this plant suggested very strongly that somatic segregation had occurred.



Text-fig. 2.
a. Fruit of *S. rosacea.* (× 6.) *b.* Fruit of F_1. (× 6.)
c. Fruit of *S. granulata.* (× 6.)
In *a*, *b*, and *c* the persistent sepals and filaments have been removed.

SUMMARY.

1. *Saxifraga granulata* and *S. rosacea* are distinct species. The chief differences are in habit (bulbils in *S. granulata*, whose shoots die down after flowering, sterile rosettes in *S. rosacea*, which is evergreen), sepal shape, petal shape, and fruit shape. Subsidiary differences, not absolutely definite and constant, are found in flower-size, venation of petals, stigma shape and size, and size of seed.

2. The F_1 generation is so uniform that it only shows fluctuations equivalent to those found in selfed lines from the parents, except in one plant with sepaloid to tubular petals. The plants remain evergreen or nearly so, but the size and form are more nearly those of the pollen parent (*S. granulata*) than of the ovule parent (*S. rosacea*). Sepal shape is intermediate; petal shape is intermediate, but verging towards *S. rosacea*; fruit shape and seed size are as in *S. rosacea*.

3. Large generations of F_2 and F_3 are extremely uniform, except for minor individual fluctuations and for the occurrence of lobed or stamin-odal petals in certain plants. The plants are very like those of F_1, except that there is a tendency for the formation of larger flowers and larger fruits.

4. Sepaloid to tubular petals and reduced stamens appeared in one F_1 plant. In F_2 the following variations appeared, each in several individuals:

(i) Lobing of petals.
(ii) Staminody of petals.

The latter reappeared in F_3 generations, with one exception. Its occurrence in a large majority of plants in one F_3 generation from a plant of F_2 with staminodal petals suggests that the character may have a genetical basis.

5. The non-segregating into parental characters in F_2 and F_3 led to the suggestion that these were tetraploid, and this has been confirmed by the cytological investigations detailed in the following paper.

EXPLANATION OF PLATES.

PLATE III.

Saxifraga rosacea.

PLATE IV.

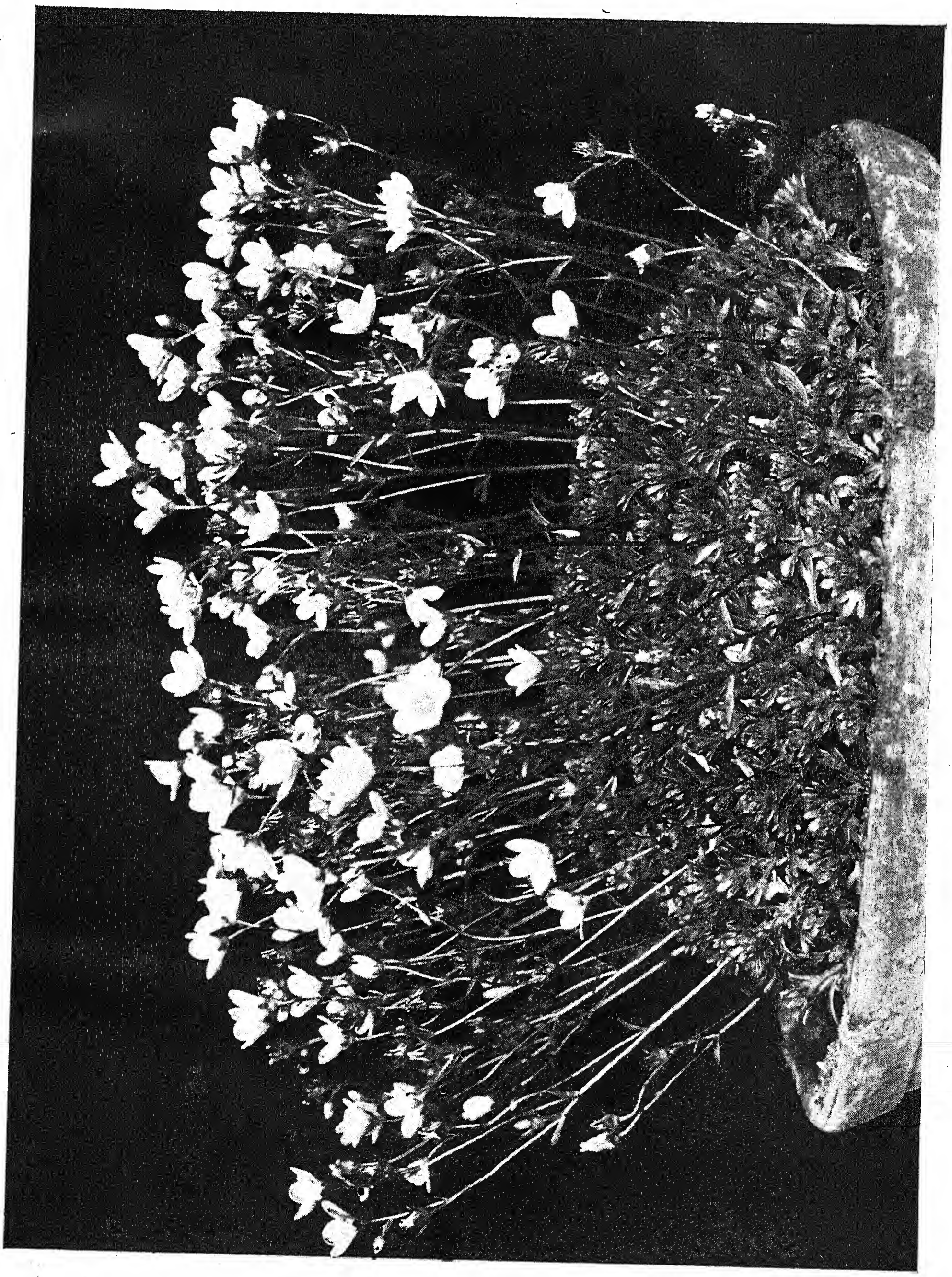
Saxifraga granulata.

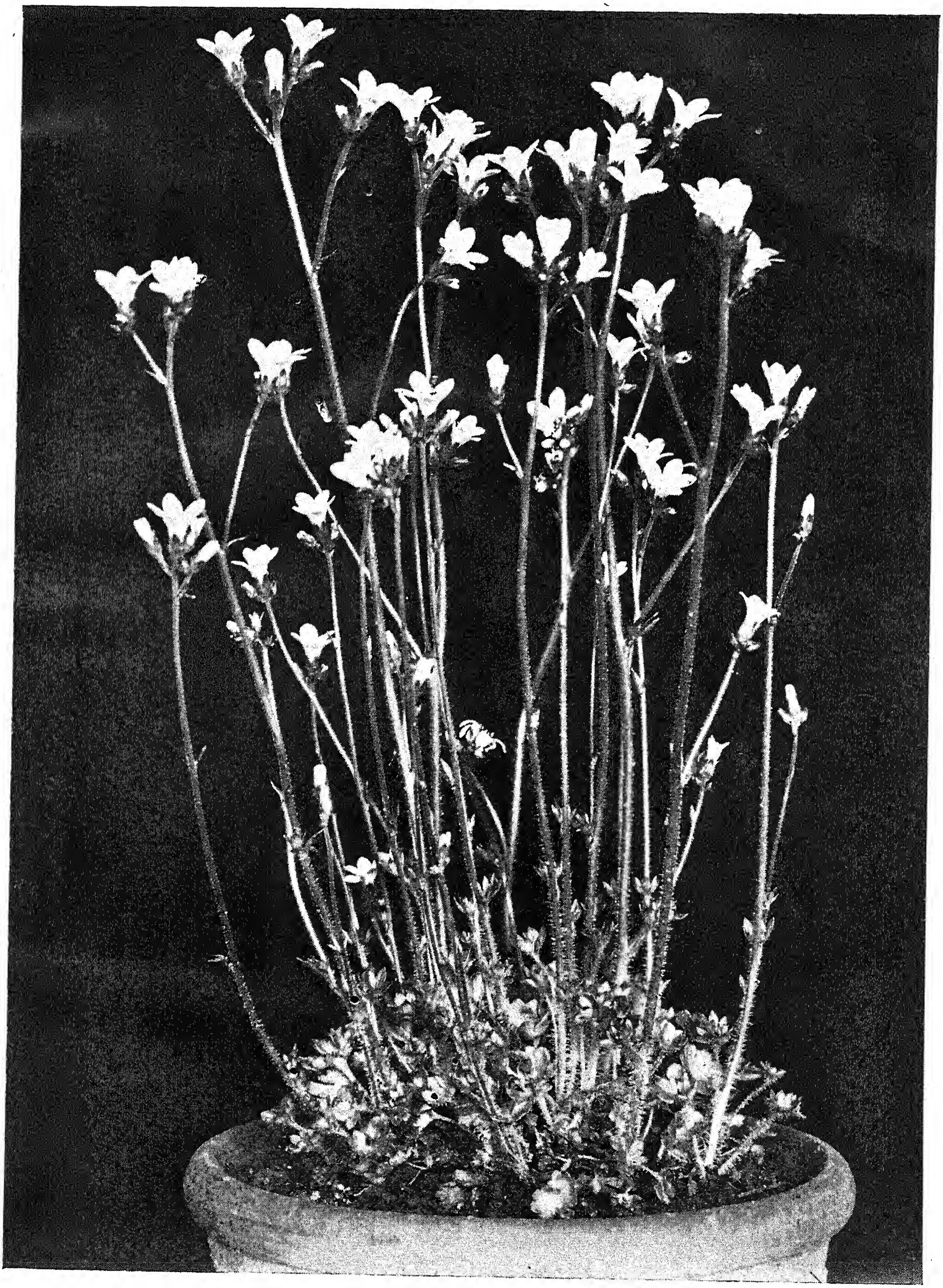
PLATE V.

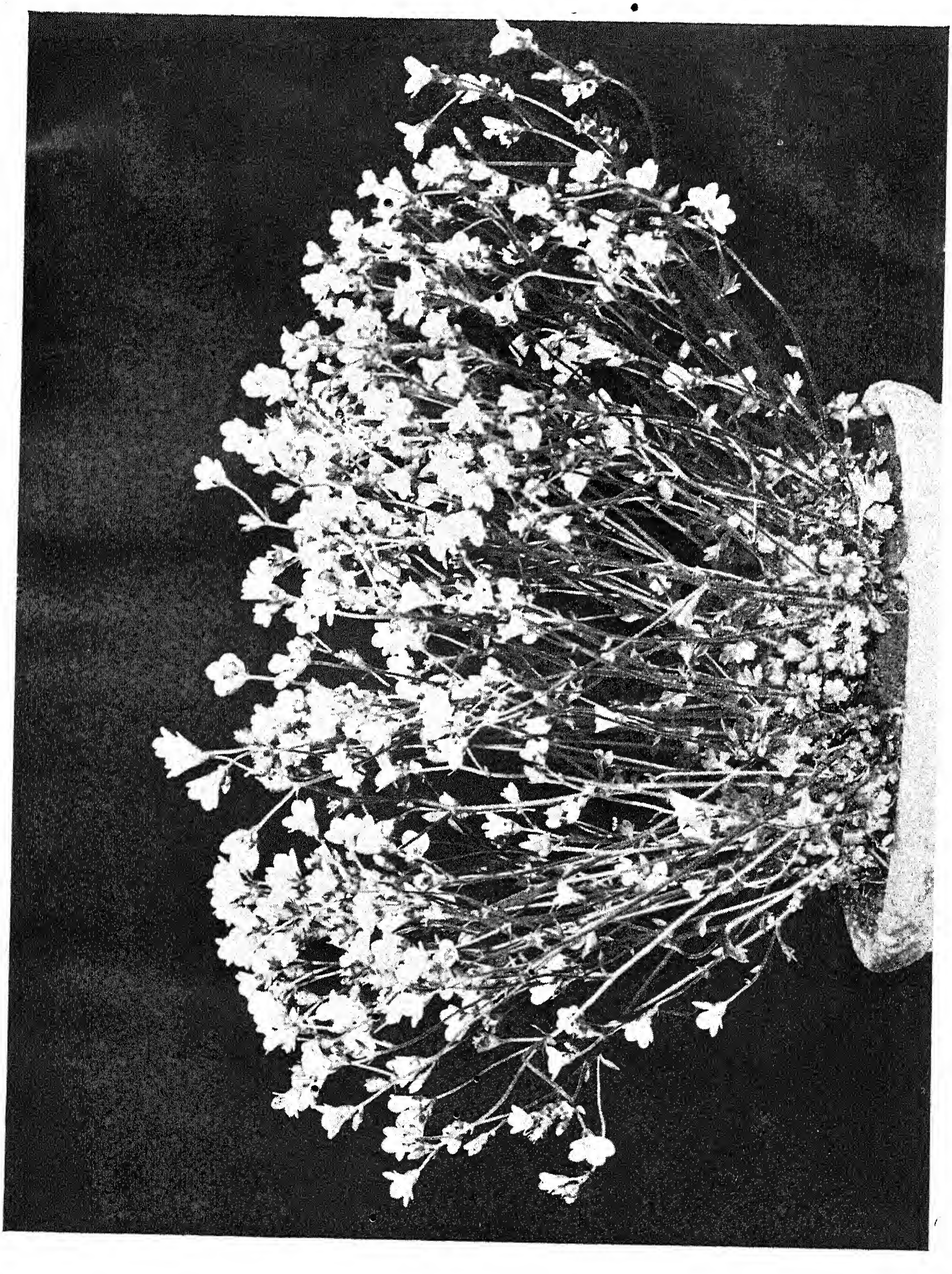
Saxifraga rosacea ♀ × *granulata* ♂, F_1.

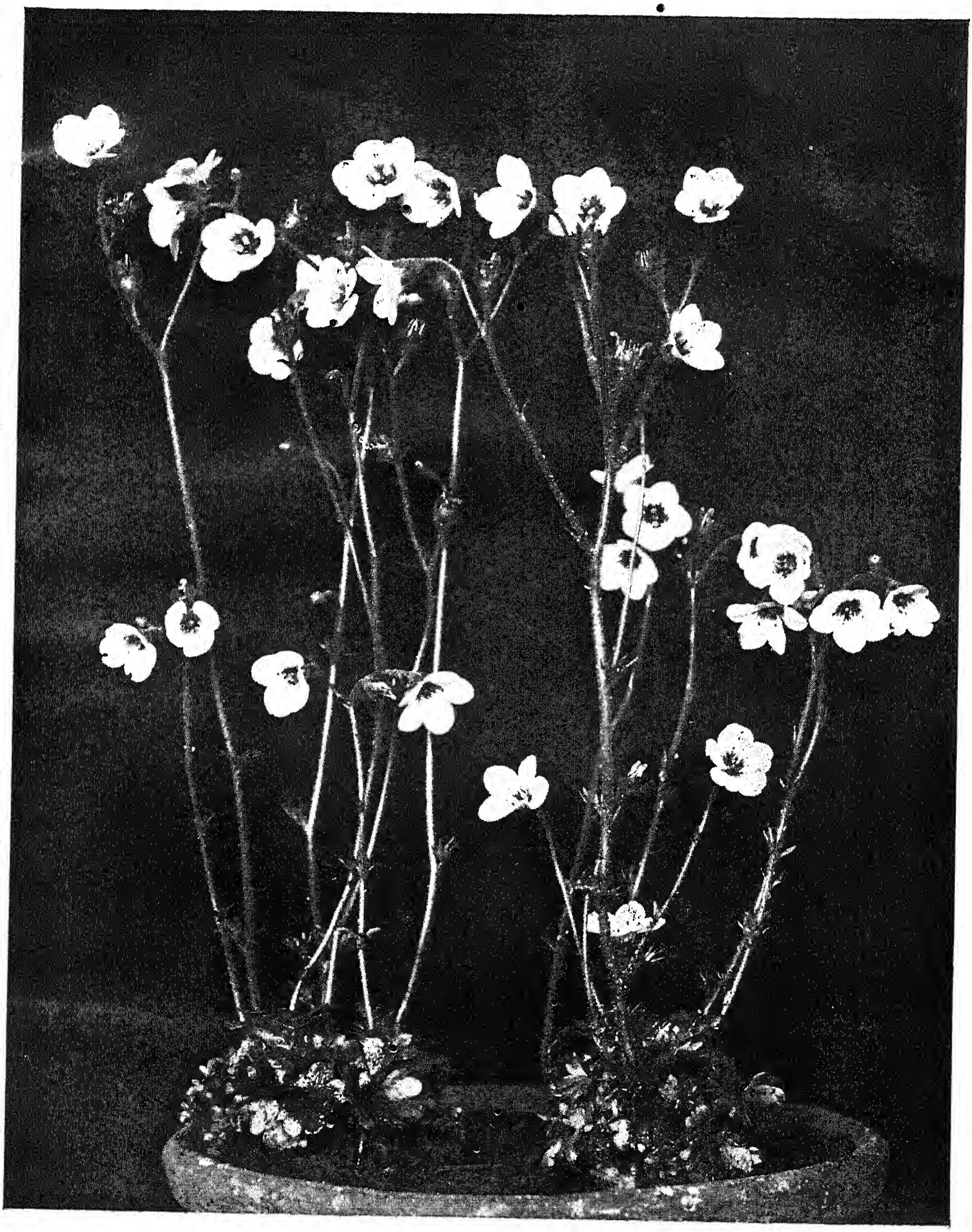
PLATE VI.

Saxifraga potternensis, F_2 from original cross.









STERILITY AND FLORAL ABNORMALITY IN THE TETRAPLOID *SAXIFRAGA POTTERNENSIS*.

By R. O. WHYTE.

(With Twenty-nine Text-figures.)

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I. Introduction.

During the following researches, in addition to the meiotic phenomena associated with a semi-heterotypic division and the production of a tetraploid F_2 generation, other features of interest have arisen. In the

F_1 and succeeding generations, plants have occurred which produce deficient flowers; anther deficient in some examples, and ovule and petal deficient in others. These types are described in detail in the account of the filial generations. In order that the phenomena may be better understood, a considerable section has been introduced dealing with similar observations in a number of other genera. This is followed by a hypothesis to account for the production of the abnormal types. Finally, an attempt is made to explain the floral deficiency encountered in *S. potternensis* by the application of the results obtained in the examination of the other similar, but less complicated, types.

II. Material and methods.

The necessary cytological material was collected from numerous plants, specially selected at Potterne as examples of the new types which have arisen in the breeding experiments on the genus *Saxifraga*, and grown subsequently in the Cambridge Botanic Garden. Various plants are described by the use of certain numbers which refer to the method of recording adopted in the experimental ground, and the vegetative characters and genetical behaviour of the plants will be found in the first paper of this series[1] under similar heads.

The fixations were made with the Carnoy and formalin-chrom-acetic combination used in the *Ranunculus* work (Whyte, 1929 *b*), and the general results were satisfactory. Skovsted (1929), who is apparently using the same fixative, also reports good results. As before, gentian violet was used, on this occasion to the exclusion of other methods. Sections were cut at 13μ.

III. Parental species.

(1) *Meiosis.*

No difference has been noted in the meiotic phases of *Saxifraga rosacea* and *S. granulata*, the parent species concerned in the origin of *S. potternensis*. The account refers, therefore, to either species. The results obtained with the fixative mentioned above are similar in some ways to those obtained in smear material; especially is this the case in early prophase, where the almost complete absence of the synizetic knot is an important feature. This absence of a "contraction stage" has been noted by Newton (1926) in the prophase of *Tulipa*, while Darlington (1929) discusses the appearance of this stage in *Hyacinthus*. Owing to

[1] See E. M. Marsden-Jones and W. B. Turrill in this *Journal*, vol. XXIII, p. 83.

the rather small size of the cells in *Saxifraga* and the thin nature of the threads found in the early prophase nuclei, it is very difficult to say whether there is any pairing at this stage. During later prophase the thread appears homogeneous throughout, except in rare instances when some suggestion of internal structure is to be seen in the spireme. The results, however, are not conclusive. The latest work on chromosome pairing (Darlington, 1929) shows that definite conclusions are inadvisable unless the material studied is suitable in every way for a detailed examination. Since this cannot be said for *Saxifraga*, and since this aspect of the problem is rather subsidiary in the present study, it will not be enlarged upon.

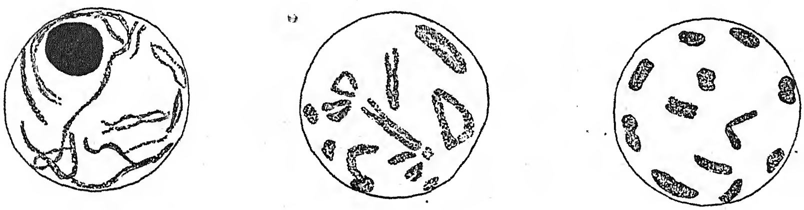

Fig. 1. Fig. 2. Fig. 3.

Figs. 1, 2, 3. *S. granulata.* Late prophase up to diakinesis. (× 2200.)

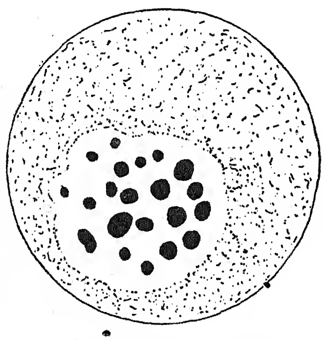

Fig. 4. *S. granulata.* Heterotype plate in pollen mother cell. (× 2200.)

By marked condensation and shortening of the pairing chromosomes, the nuclei take up the arrangement normal for diakinesis (Figs. 1, 2, 3). After the dissolution of the nuclear membrane in the pollen mother cells the chromosomes assume their positions on the equatorial plate (Fig. 4). In polar view this plate is regular and compact. Actual counts, however, are often difficult to make, owing to the fact that some homologous univalents, although lying in close juxtaposition on the plate, are apt

to be counted as whole chromosomes instead of as members of a pair. This may be regarded as the result of loose pairing in prophase, or as early evidence of the heterotype split in certain bivalents. As a result of this arrangement, counts ranging from 16 to 22 are obtainable according to the pollen mother cell in question. After examination of numerous plates and comparisons with the size of the bivalents at diakinesis, it is possible to say that the haploid chromosome number is

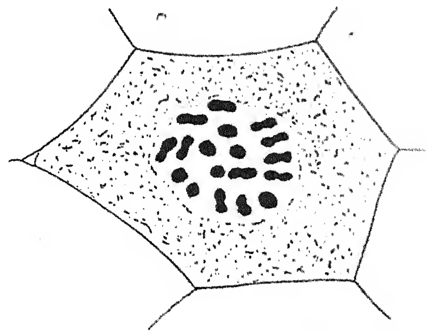

Fig. 5. *S. granulata.* Heterotype plate in megaspore mother cell. ($\times$ 2200.)

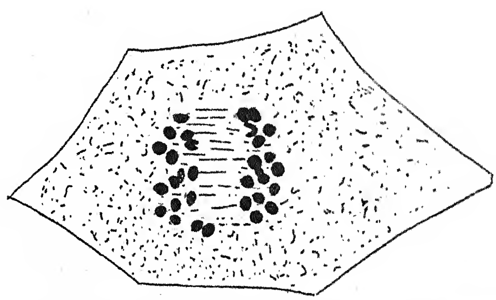

Fig. 6. *S. granulata.* Heterotype division in megaspore mother cell. ($\times$ 2200.)

about 16. In a cytological study of these species, Schurhoff (1925) gives a similar explanation for the variation in the number of chromosomes on the plate, and concludes that the chromosome number for *S. granulata* and *S. rosacea* (*S. decipiens*) is 16. The heterotype divisions are regular and are followed by a definite resting stage in interkinesis, when the individuality of the chromosomes is quite lost.

Meiosis in the megaspore mother cell is similar in all essential details, but counts of 16 are more frequent. No later stage than that with the four megaspores has been studied.

IV. F_1 GENERATION PLANTS.

(1) *Meiosis*

The pollen mother cells pass through prophase in a normal manner, and there is a considerable degree of pairing (Fig. 7). The heterotype plate, however, is very irregular in arrangement, some chromosomes dividing and commencing to move towards the poles before the plate is actually formed, thus rendering accurate counts almost impossible. From side views of this division it is evident that the great majority of the bivalents have been formed normally in the previous prophase and that, so far as chromosome complements are concerned, incompatibility is not very marked. The reduction division is of a very irregular nature. Some chromosomes pass early to the poles, to be followed later by the majority of the remainder; finally the lagging members may commence to move towards the poles. The ultimate result of this division depends

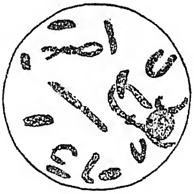

Fig. 7. *Saxifraga* F_1 generation. Diakinesis in pollen mother cell. (× 2200.)

entirely on the stage the various pollen mother cells in a given anther loculus have reached when the time to form dyads, or the influence causing the return from a dividing period to a resting stage arrives. This factor decides whether they shall form the normal parental type of interkinetic nucleus, possibly leaving some lagging univalents in the cytoplasm, or whether the chromosomes shall become reconstituted as a single nucleus, thereby annulling the reduction division. An anther loculus examined after this division shows many dyads with their nuclei in the typical interkinesis and a few pollen mother cells with a single nucleus, generally recognisable as being slightly larger than those of the dyads. The cytoplasm of the normal dyads contains numerous lagging chromosomes which disappear or lose their staining reactions before the final tetrads are formed. The other uninucleate pollen mother cells with the diploid number of chromosomes generally show that the stray members of the complement have been absorbed in the reconstituted nucleus, the cytoplasm being free from such bodies. When the next

anther loculus, when the "resting period" has passed and a "dividing period" commenced. The pollen mother cells shown cannot be regarded as being in a direct sequence with the types described above. Fig. 14 shows the two homotype nuclei as separate entities, but the small chromatin group in the cytoplasm is evidence of lagging in the previous heterotype metaphase. In Figs. 15 and 16, the telophase nuclei have been linked by a chromatin band, one aspect of the lagging phenomenon, and this connection has not been severed during interkinesis. In the following

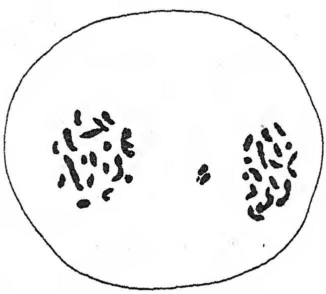

Fig. 14.

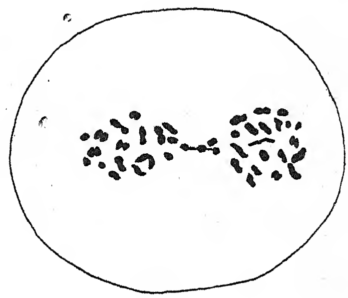

Fig. 15.

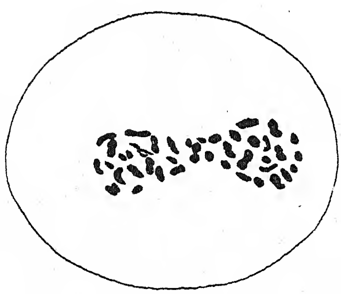

Fig. 16.

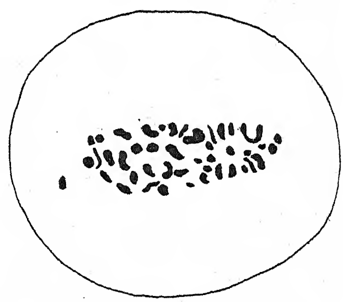

Fig. 17.

Figs. 14, 15, 16, 17. *Saxifraga* F_1 generation. Homotype divisions, showing gradations from the almost normal state in Fig. 14 to the abnormal unreduced nucleus in Fig. 17. (× 2200.)

homotype division figured here, the homotype plates are linked, to a slight extent in Fig. 15, but by a considerable connection in Fig. 16. It is probable that two spindles would have been formed in the pollen mother cell shown in Fig. 15, but it is doubtful what would have occurred in the other cell (Fig. 16). Fig. 17 shows what may be regarded as the homotype division of the reconstituted nucleus. If this can include the single chromosome which is apparently separate from the main group in the homotype separation, the result should be quite regular.

It has been suggested or implied in the above account of meiosis in the F_1 generation that a definite influence is present in the anthers, dividing the meiotic process into certain periods termed "resting" and "dividing" respectively. It is stated that the pollen mother cells in a given anther loculus enter a resting stage regardless of the point they may have reached in the heterotype division, thereby causing the appearance of normal dyads or reconstitution nuclei, as the case may be. A second "dividing period" is then assumed, causing the completion of the homotype division. This point will be taken up in a later part of the paper (see p. 119).

(2) *Anther deficiency.*

Among the plants of the F_1 generation sent from Potterne was a specimen (B 2 F_1 Plant 8) which was described as "sterile," no seed being set when "selfed." When other pollen was admitted, abundant seed was formed.

The anthers of the flowers collected were found to be formed quite normally so far as the general delimitation of the sporogenous tissue and tapetum is concerned. The examination of the prophase stages, however, showed that while some were normal in appearance, the majority showed abnormalities of one kind or another. All grades of aberrant types were to be seen in different flowers. The more favourable examples showed pollen mother cells in normal prophase, surrounded by healthy, deeply staining and presumably active tapetum. The presence of some few flowers with pollen, sometimes quite normal in appearance, indicates that the reduction divisions had on occasion been completed. In the same collection one may find flowers which appear incapable of passing out of the early prophase in their meiotic process in the anthers. These have pollen mother cells and tapetum as yet normal in appearance and staining qualities, but in spite of the rapid vegetative development going on in the ovary the sporogenous tissue in the anthers appears to be unable to enter upon the reduction phase. The next type of flower noted shows the pollen mother cells in a normal condition but surrounded by a tapetum which, by its inability to stain properly, suggests an inactive state. The last stages of this process are found in anthers with an inactive and disintegrating tapetum, surrounding sporogenous tissue in various degrees of disorganisation. A considerable reduction in the volume of the nucleus, until the chromatin of the prophase spireme is coagulated into a small dark-staining mass in the centre of the cell, characterises the collapse of the pollen mother cells. This anther deficiency is some-

times distinctly progressive, commencing in a single loculus of an anther, spreading to the other loculi of the same or neighbouring anthers until they gradually become affected throughout the flower. The possibility that variation in penetration of the fixing reagents may be the cause of these irregularities has been carefully considered, but no evidence was found which might support this suggestion. In all the collections of cytological material, the fixing solution and subsequent treatment were absolutely standard throughout, and it would be difficult to interpret the abnormal flowers observed in any other way than as evidence of some fundamental defect in the plants in question.

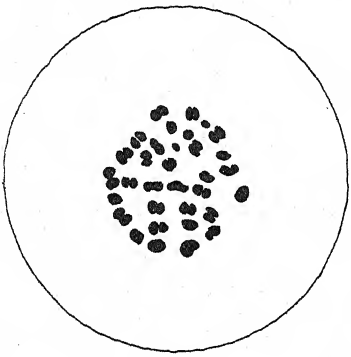

Fig. 18.

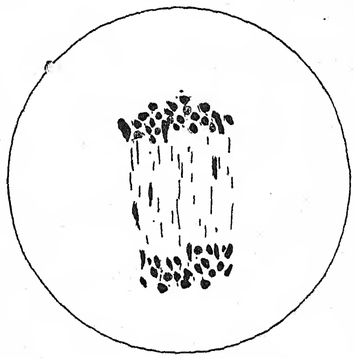

Fig. 19.

Fig. 18. *Saxifraga* F_2 generation. Heterotype plate in pollen mother cell. (× 2200.)
Fig. 19. *Saxifraga* F_2 generation. Heterotype division. (× 2200.)

Ovule development in the same flowers was found to be quite normal, and directly comparable with the parental type. Prophase and heterotype divisions are passed through in the manner normal for an F_1 plant. Sufficient views were not obtainable to decide how the semi-heterotypic division takes place in the megaspore mother cell.

The sterility of the plant under consideration is therefore assumed to be due to anther deficiency, to the inability of the pollen mother cells to develop owing to lack of suitable supplies from the tapetum at the critical juncture. The great preponderance of anther deficient flowers suggests that the occurrence of a few flowers (not more than two or three were noted) with good pollen is to be regarded as an exception due to the temporary absence of the influence which causes this anther degeneration. There is a possibility that good pollen production will be found only in the "primary" flowers on an anther deficient *Saxifraga* plant. The classification of the flowers on a given plant in order of their importance, as been done by Darrow (1929) in *Fragaria*, is being studied.

(3) *Ovule and petal deficiency: Petal metamorphosis.*

Another plant with flowers of an abnormal character was examined in the F_1 generation. This specimen (B 2 F_1 Plant 3) was bracketed with an F_2 generation plant (B 2 F_2 Plant 6) as having flowers with abnormal petals, these parts being much reduced. The collections were made from these two plants, and preparations examined before the types had finished flowering. The flowers collected from the first plant were found to present certain features which will later be considered as possibly explaining the occurrence of abnormal petals. The material from the F_2 generation plant did not show similar features and did not, therefore, bear out the provisional explanation mentioned. On examining the plants in full flower in Cambridge, however, it was found that, while B 2 F_1 Plant 3 had petals abnormal in character, B 2 F_2 Plant 6 had normal petals in every flower examined.

It was then learned from Potterne that the plant from which the Cambridge bulbils had been taken had been found to produce bulbils of three distinct types. The bulbils from one part of the original plant produced plants bearing normal flowers, while the other two sets of bulbils produced plants bearing flowers with deficient or metamorphosed petals. It seems evident that the Cambridge F_2 (presumed) petal-deficient plant had come from the first set of bulbils. One would not, therefore, expect to find the floral development similar to that of B 2 F_1 Plant 3.

It is necessary at this point to state why the terms "petal deficiency" and "petal metamorphosis" have been introduced, and what the relation between the two terms is assumed to be. Petal deficiency is comparable with anther deficiency, and covers a reduction from the normal state to the almost total extinction of these floral parts. It will be noted in a later part of this paper that the phenomenon occurs in some material of *Silene maritima* that has been examined. In the *Silene* collections, it is merely petal deficiency that has been found up to the present time. In *Saxifraga*, however, true petal deficiency can be assumed only in the very early stages of the reduction of these floral parts. When this deficiency has gone so far, a second feature, probably a direct result of the first, arises. This is the petal metamorphosis described in various parts of the genetical paper on this subject. This phenomenon is not yet properly understood, but certain points have arisen which may be used in future investigations. These will be noted as they arise in later sections of the present paper.

To return to B 2 F_1 Plant 3, prophase in the pollen mother cells proceeds in a normal manner in the great majority of the examples, and pollen is formed. It was found that the ovary was abnormal. In the development of a typical ovary, *e.g.* *S. granulata*, during the early prophase stages of meiosis in the pollen mother cells, the placentae, examined in radial longitudinal section, commence development as two crescent-shaped zones of meristematic tissue. These grow outwards for some time, the crescentic outline of the advancing growth, as seen in section, extending without losing its unbroken contour. Small protuberances, the rudimentary ovules, then appear on the developing

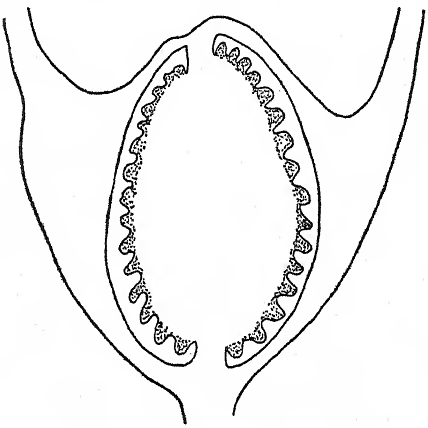

Fig. 20.

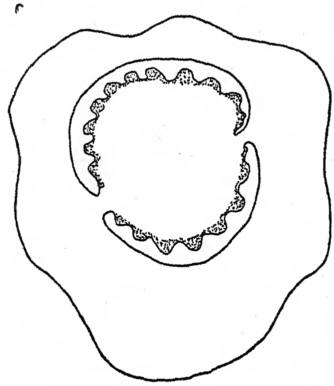

Fig. 21.

Fig. 20. *Saxifraga granulata.* Normal placental development, longitudinal section. (× 20.)
Fig. 21. Transverse section of same. (× 20.)

placenta and grow in the same direction as the general growth has been proceeding, *i.e.* outwards to the ovary wall (Figs. 20, 21). It is at this stage that the megaspore mother cell is delimited, the nucleus remaining in early prophase for some time. The ovules become flexed upon themselves to take up the form of the mature ovules of the species; the integuments are formed and the megaspore mother cell passes through the reduction division.

But in the petal-deficient type of flower the ovaries show little or no development of the placenta and ovules. Radial longitudinal sections of one of these completely "ovule-deficient" flowers show the two cavities on either side of a central column of non-meristematic tissue containing the vascular supply of the placental region (Fig. 24). All gradations between this very reduced type and other more favourable examples

with considerable ovule development are to be found. Numerous remarkable types of deformed ovary growth have been noted: some flowers show the column mentioned above as feebly developed in the lower regions of the ovary, but expanded above into a reduced placental area bearing ovules (Figs. 22, 23); in other flowers the column is undeveloped almost to the upper limits of the ovary. But before this latter

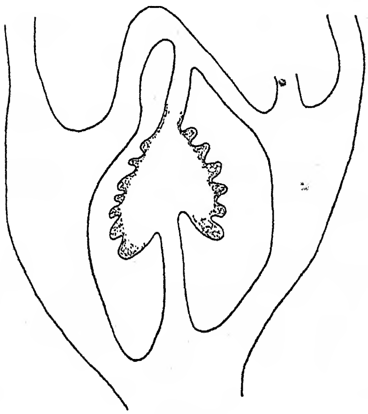

Fig. 22.

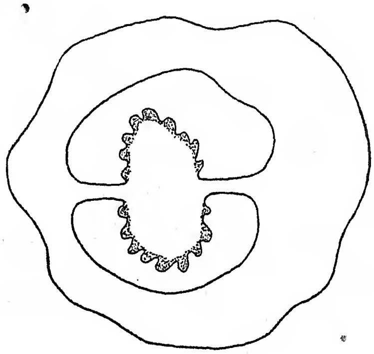

Fig. 23.

Figs. 22, 23. *Saxifraga* B 2 F_1 Plant 3. Abnormal type of placental growth in longitudinal and transverse section. (× 20.)

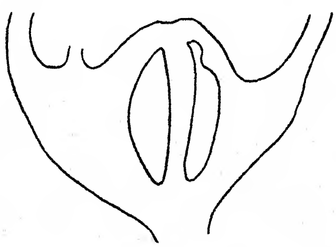

Fig. 24.

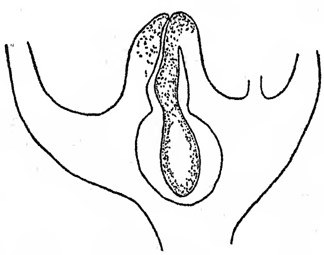

Fig. 25.

Fig. 24. *Saxifraga* B 2 F_1 Plant 3. Ovary lacking meristematic activity in placenta. (× 20.)

Fig. 25. *Saxifraga* B 2 F_1 Plant 3. Longitudinal section through ovary with abnormal placental growth described in text. (× 20.)

region of the placenta has lost its meristematic powers, a remarkable growth arises as a protuberance at this point, and grows down into the empty cavity of the ovary (Fig. 25). This may eventually develop ovules with normal megaspore mother cells.

Ovule deficiency in B 2 F_1 Plant 3 is very marked, and there appears to be a correlation between petal and ovule development. For flowers

with good petal development generally show the most reduced type of ovule development, and conversely the most reduced petals are associated with considerable placental activity. This generalisation does not apply when petal metamorphosis is present.

It is further to be noted that, in the flowers with the most reduced ovaries, anther deficiency is also to be found. The cause of this is not quite clear at the moment. It may be explained by the hypothesis suggested below but, on the other hand, it may be that the excessive formation of gum in the vessels of the vascular bundles supplying all parts of the flower has some relation to staminal failure. For the vascular supply to the undeveloped placental region in the flowers just described is choked with gum, while the cells of the placenta which have lost their meristematic powers have also gum deposits.

V. F_2 GENERATION PLANTS.

(1) *Meiosis.*

In the pollen mother cells examined the meiotic prophase was of the normal type. There is good evidence of pairing, and the plates (Fig. 18) with the tetraploid number of chromosomes are regular and more suitable for counting than those of F_1 plants. The haploid chromosome number is 32 to 36, the figure tending to vary for the same reason as was indicated for the parent species. On a few plates there was a tendency to form quadrivalents; seldom were more than two such associations observed. The movement to opposite poles is not yet quite regular (Fig. 19), several chromosomes leaving the plate before the main body, while others tend to lag. At the interkinetic resting stage, however, lagging univalents in the cytoplasm are not common.

(2) *Anther deficiency.*

No specimen of the "sterile" type was included among the F_2 plants studied for comparison with the "anther-deficient" F_1 plant already described. In working through the material, however, it was noticed that one example (B 2 F_2 Plant 4) showed a marked tendency towards such a state. The characteristics of anther degeneration were present, and several flowers showed completely sterile anthers. Sterility in this plant did not, however, approach the F_1 type, and would probably pass unnoticed in field observations. With foreign pollen seed production was excellent in quantity and quality, as was also found for the anther-deficient F_1 plant.

(3) *Petal deficiency: Petal metamorphosis.*

Petal deficiency in its simple state has not been found in the F_2 generation; as described in the genetical paper on this subject, various degrees of petal metamorphosis occur. This aspect of the subject is not yet properly understood, but it seems evident that a petal "metamorphosed" into some other floral part does not exert the same influence in competitive development (discussed below) as has been described for the reduced petals of the F_1 generation.

VI. F_3 GENERATION PLANTS.

Meiosis in the pollen mother cells of these plants approaches very nearly to the parental type, divisions being much more regular. The chromosome number is similar to that of the F_2 generation.

Only on rare occasions were examples of anther deficiency found. A collection from B 2 F_3 Plant 10, in which the petals had become metamorphosed into stamens, showed every type of staminoid petal. Many resembled those abnormal floral parts figured in the Double Stock (Corner, 1927); others were more staminoid, but to be distinguished from the normal stamens by the presence of two large loculi in place of four smaller loculi.

VII. A COMPETITIVE INFLUENCE IN FLORAL DEVELOPMENT.

(1) *Introduction.*

In recent work on *Silene* and *Ranunculus* (Whyte, 1929 *a* and *b*), a "time factor" was postulated to account for certain aberrant types of floral morphology. The hypothesis of competitive development was found to explain the phenomena tolerably well, and has since been applied to similar abnormalities in other genera. We may consider it also in connection with the *Saxifraga* problem. Here the terms "anther deficient," "ovule deficient" and "petal deficient" have been used, the first two having been adopted in preference to the usual terminology employed in the study of abnormal floral types. Such terms as "male," "female," "staminate" and "pistillate," "gynodioecism" and "andro-dioecism," "male sterile" and "female sterile" have been abandoned in favour of those suggested. In *Saxifraga*, the three types of floral deficiency are linked up with each other, and a common terminology is desirable. The term "deficiency" is restricted at present to cover only true reduction of floral parts, either in size or stage

of development reached. Metamorphosis of parts in any of its aspects is not to be considered as directly similar, although it may well be a derived condition.

(2) *Ranunculus acris.*

This was the first plant in which the change in developmental sequence of the reproductive parts of the flower was noted (Whyte, 1929 *b*). Owing, probably, to the very considerable somatic growth associated with ovule development in *Ranunculus*, the first traces of the ovules do not appear in a normal hermaphrodite flower until pollen development is almost or quite complete. There is thus a considerable interval between the reduction processes in the sporogenous cells in the anthers and ovules of any given flower. In the "female" or "totally anther-deficient" flower, the reduction processes were found to coincide,

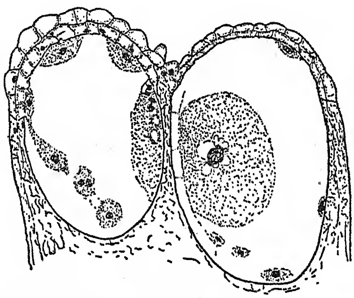

Fig. 26. *Ranunculus acris.* Tapetal plasmodium in "abnormal" plant (Whyte, 1929 *b*). (× 166.)

and it was concluded that this change has a retarding effect upon the anthers, which is expressed in widespread tapetal failure and consequent degeneration of the pollen mother cells before pollen formation. This suggested explanation is supported by evidence from the intermediate types (Fig. 26), in which the anther deficiency is not so marked, and in which a quantity of good pollen is found. In these plants the interval between the two reduction processes has been reduced without actual coincidence. There is a direct correlation between the amount of overlap of anther and ovule phases on the one hand, and the stage of development reached in the anthers on the other.

(3) *Silene maritima.*

Anther deficiency was found to be marked in a plant ("female" A 2) examined at Potterne (Whyte, 1929 *a*). The reduction of the interval

between the meiotic processes in anthers and ovules was not so marked, and tapetal failure generally took place when the pollen sacs contained immature pollen. Cytological observations also showed that certain plants (*S. maritima* A 1) which had been classed as hermaphrodite in the field were examples of mild anther deficiency, the tapetum tending to cease functioning when only a small quantity of mature pollen grains was formed. It was known (Marsden-Jones and Turrill, 1928) that the anther-deficient ("female") type might, on occasion, cross a postulated anther fertility line and produce hermaphrodite flowers. This is to be explained by a temporary increase in the interval between reduction processes, with tapetal activity extending sufficiently to form a little good pollen. Conversely, it was subsequently suggested from the cytological evidence that the offspring of *S. maritima* A 1 might as readily cross the postulated line and produce totally anther-deficient flowers, without pollen. This forecast proved to be true, for in the dry season of the following summer, a large number of "female" flowers were reported from the plants concerned.

Petal deficiency is also being studied in these *Silene* plants. No examples of petal metamorphosis, which might be compared with the *Saxifraga* types, have been noted up to the present, but a feature has arisen which may be of some importance in this connection. In the petal-deficient *Silene* flowers, examination of the young undeveloped petal made while the ovules are actively developing and forming embryo sacs shows that the cells in the upper region of the petal are shrivelled and dead. These should normally be in a healthy condition, capable of becoming actively meristematic when the supplies of suitable nutriment pass along the petal bundles in quantity at the conclusion of the ovule development phase. Their premature death, probably through starvation, causes the absence of any meristematic activity in these parts, and no petal expansion phase is found. Hence the flowers are petal deficient. Active meristematic growth does, however, commence at the base of, and in the axil of, the abortive petal, and the vascular bundle supply tends to be diverted in the direction of the new growth. No example has been noted in which this secondary development has proceeded far, so that we have as yet no indication of what type of floral part it is capable of forming.

(4) *Centaurea: Triticum.*

In the preceding paragraphs it has been suggested that there is always a considerable interval between the meiotic processes in the anthers and

ovules, and that it is the reduction of this interval which causes the total or partial failure of one or other of the reproductive parts. This suggestion applies only to those floral types with considerable ovule development, such as might be supposed to place a marked physiological strain on the organisation of the flower. With *Ranunculus* and *Silene* may be classed *Bomarea* (cf. p. 113). *Centaurea* and *Triticum* belong to the "few ovules" class, and we find that the reduction processes may proceed almost concurrently in the anthers and ovules of normal hermaphrodite flowers without any harmful effect on the floral development. (This applies only to the central disc florets of certain plants of *Centaurea* examined.)

(5) *Plantago: Veronica.*

In these protogynous types the reduction processes coincide, and the rapid growth of the style is probably associated with the earlier maturing of the ovary. These two genera, together with *Aesculus* (cf. below), belong to the class with few ovules mentioned above. Hence no broad generalisation on protogynous flowers is possible without further study.

(6) *Aesculus Hippocastanum.*

Rendle (1925) states (pp. 300–1) that "the large pyramidal inflorescence is a mixed one consisting of a number of scorpioid cymes arranged in a panicle; it is known as a thyrsus....The flowers are andro-monoecious, the male flowers, in which a rudimentary ovary is present, often open first. Generally some of the bisexual flowers are biologically female from the premature dropping of the anthers. The bisexual flowers are proterogynous; in the first stage the stamens are bent sharply downwards while the style projects in a long ascending curve, in the second, or male stage, the stamens rise almost to a horizontal position....Generally only one ovule in the ovary develops into a seed, two out of the three ovary-chambers becoming crushed by the considerable growth of the one containing the very large seed."

Material for the study of floral development was collected as follows. Buds were obtained from the upper regions of the inflorescence, the flowers of which are predominantly ovule deficient, at the time when reduction divisions might be presumed to be in progress, and again when the buds were quite mature but unopened. Similar collections were made from the lower regions of the inflorescence where the flowers are predominantly hermaphrodite.

Flowers taken from both upper and lower regions developed normally

up to the formation of the pollen mother cells and the megaspore mother cells, and were of the protogynous type, with coincident divisions. The meiotic processes were normal and concurrent in the lower regions of the inflorescence, abundant pollen and normal embryo sacs being formed. In the flowers of the upper region, the process is not so regular. Both anthers and ovules reach the prophase of meiosis in the sporogenous cells normally, but only the pollen mother cells continue development. Almost immediately after the commencement of meiosis in the anthers, widespread degeneration of somatic nuclei is to be seen in the ovules which up to this point were healthy, taking up stains well and frequently undergoing mitosis. All divisions cease, and the nuclei assume a generally unhealthy aspect. The megaspore mother cell remains normal

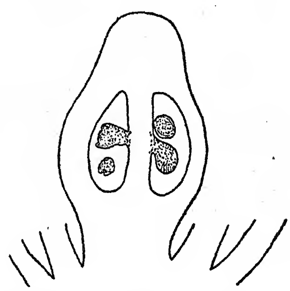

Fig. 27. *Aesculus Hippocastanum.* Ovary of young flower at stage when competition with the anthers may occur. (× 20.)

in appearance for some time in the midst of this general disintegration, but later loses staining power and collapses. The final aspect of the ovules of an ovule-deficient flower is that of groups of dead and shrivelled cells, without trace of nuclei; the ovary itself enlarges to some extent, but the style is not formed.

Intermediate stages may exist between the two extremes, the perfect hermaphrodite and the ovule-deficient type. Ovules are seen which appear to have proceeded to some extent in their further development from the reduction period, only to commence degeneration later in the manner indicated above. Others again develop further, but may not form good embryo sacs.

Fig. 27 shows the ovary of a young *Aesculus* flower which has passed the reduction phase in the anthers and formed pollen. Since the ovules are still in a healthy condition and embryo-sac formation is proceeding normally, it is evident that there is every prospect of this flower becoming normally hermaphrodite on reaching maturity. If it had been taken

from the upper regions, degeneration of somatic nuclei would already be apparent at a similar stage. Figs. 28 and 29 show the mature condition in a normal hermaphrodite and an ovule-deficient flower respectively.

The fact that the "male" flowers often open first, as stated by Rendle (1925), might be explained as being indirectly due to competitive influence in the development of the flowers. After pollen formation in the anthers, there is no meristematic tissue remaining in the ovules, and

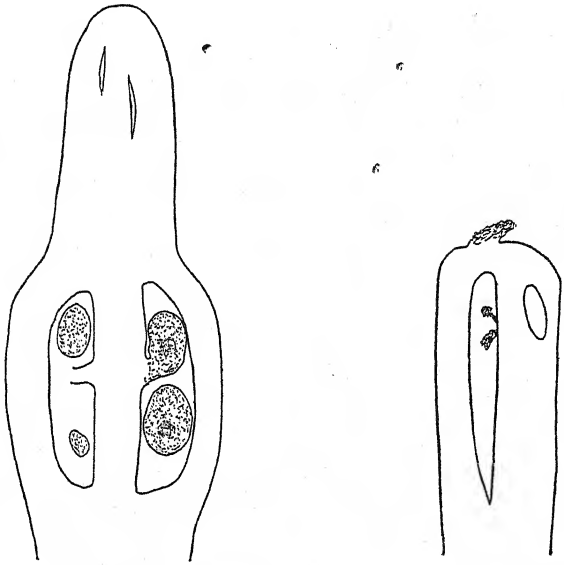

Fig. 28. Fig. 29.

Fig. 28. *Aesculus Hippocastanum.* Ovary of mature hermaphrodite flower from lower regions of inflorescence. (× 20.)

Fig. 29. *Aesculus Hippocastanum.* Ovary of ovule-deficient flower. (× 20.)

therefore no demand for food supplies. The petal expansion phase, assuming this to cause the opening of the flowers, will therefore commence earlier owing to the elimination of the ovule development phase by competition.

(7) *Asparagus officinalis.*

Shoji and Nakamura (1928) described in detail the degeneration and abortion of floral parts, and concluded that "the too early degeneration of tapetal cells is one of the factors which bring about the degeneration of the pollen mother cells."

Examination of some deficient material growing in the Cambridge Botanic Garden showed similar features. Apparently the rule in this

species is that the reduction processes coincide, and that every type of flower can be found, from totally anther deficient (frequent) to hermaphrodite (rare) and totally ovule deficient (frequent).

The important place that the reduction division assumes in floral development is seen in this species. Two flowers from an ovule-deficient plant are especially interesting. The younger of the two showed pollen mother cells and megaspore mother cells in early prophase. The somatic nuclei in the ovules, the ovary wall and the developing style were all in excellent condition. In the second flower, the pollen mother cells had commenced meiosis; heterotype plates were frequent and the tapetal cells were apparently in a very active state. The megaspore mother cell in the same flower had not left the early prophase stage noted above; the reason for this delay was evident, for, as in *Aesculus*, the somatic nuclei in the ovules were disintegrating. The flower would therefore have been ovule deficient.

(8) *Bomarea Matthewsii.*

A peculiarity in floral development in the genus *Bomarea* has been noted (Whyte, 1929 *c*). In certain species growing in the Cambridge Botanic Garden, anther formation and meiosis proceed normally. Meiosis tends to follow parallel courses in the two whorls of stamens; the outer whorl of three may show pollen mother cells whose nuclei are dividing at the heterotype, while the inner whorl has not passed the contraction stage. In other plants there was a tendency to depart from this regular method and to develop in what might be described as a "descending series." Thus two of the outer anthers may show naturing pollen, and the other pollen tetrads; two of the inner anthers may show heterotype plates, and the other diakinesis.

In one of the hybrids made at the Glasgow Botanic Garden by Mr G. H. Banks, this tendency was found to be accentuated; the last anther had lagged so much behind the others in development that it may be regarded as having overlapped into the ovule development phase. As a consequence, the pollen mother cells in this lagging anther degenerated before the commencement of prophase. This degeneration was characterised by a marked multiplication in the number of nucleoli in the pollen mother and tapetal cells, a phenomenon noticed in numerous examples of disintegrating cells, especially in dying tapetal and root cap cells, and probably related to increase of surface to volume. The lagging anther remains as a tall staminode in the mature flower, showing on microscopic examination long strands of dead tissue which indicate

the position of the anther loculi. There would appear to be a proliferation of the general parenchyma of the anther following the collapse of the pollen mother cells, tending to compress these latter into the long strands noted. Certain irregularities may also be observed in the other anthers of the inner whorl.

(9) *Nolana.*

The types of floral deficiency described in the preceding sections are held to be due to fundamental defects in the organisation of the plants, or the parts of the plants concerned. Slight variation from the original observed state of any given plant may occur from time to time, possibly due in part to environmental changes. It is suggested, however, that there is another type of floral deficiency (especially anther deficiency) which cannot be considered as directly comparable with the above types.

During the study of *Nolana* (Whyte, 1929 *c*), numerous flowers were found in which chromatin budding, nucleolar budding, cytomixis and anther degeneration were very marked. These abnormalities had been noted by Campin (1925) in the parent species, and were observed by the writer in both parents and hybrids. It was found that chromatin or nucleolar budding (these processes may not be distinct) occurred during early prophase in anthers in which the tapetal cells were inactive, but still in a healthy condition. If the tapetal cells resumed an active state, the degree of activity being decided by staining and other comparisons, the pollen mother cells might resume their interrupted development. If, on the other hand, the tapetum began to disintegrate, cytomixis (Gates, 1911) would commence in the sporogenous tissue, and general anther degeneration would set in. The tapetum might fail at any time during pollen development; it was not possible to forecast that the flowers of a certain plant would show certain abnormalities at a given time, as would be possible in the anther deficient plants of *Ranunculus acris*, for example. On the same plant occur perfectly normal flowers, flowers with immature badly formed pollen grains and others with abnormal conditions in prophase, the point of anther development reached by any flower being governed by the condition of the tapetum.

This type of degeneration is probably not true anther deficiency, due to a fundamental inability to achieve the reduction division, but is due to temporary local conditions such as wilting, lack of sufficient light, etc. These abnormal conditions cause a plant, or part of a plant, to be in an unhealthy and less vigorous state, a condition which is expressed in tapetal inactivity, and in some examples, failure.

(10) *Miscellaneous types.*

Further examples of true floral deficiency have been examined, notably in the following plants: *Fragaria* (anther deficiency), *Rubus Idaeus* (ovule deficiency), *Mercurialis annua*, *Rumex alpinus* and *Empetrum nigrum*. With the exception of the complex type found in *Mercurialis annua*, it would appear that competitive development plays a large part in the production of many of the abnormalities observed.

VIII. DISCUSSION.

(1) *Meiosis in* S. potternensis.

The account of the heterotypic division in the pollen mother cells of the F_1 plant derived from the cross, *Saxifraga rosacea* by *S. granulata*, agrees in general with the previous descriptions of analogous examples (cf. Jørgensen (1928), Newton and Pellew (1929)). The semi-heterotypic division has been noted, together with intermediate forms of separation, and the reconstituted nucleus can be readily observed among the normal haploid dyads. In the F_2 generation (*Saxifraga potternensis*) the pollen mother cells show the tetraploid number of 32–36 chromosomes.

(2) *Fundamental deficiency in plants.*

Here the important point is the inability of certain plants to take the "peak load" necessitated by reduction divisions in the reproductive organs, it being assumed that the meiotic process as a whole, and more especially the actual reduction division, require a higher rate of metabolism or supply of energy than ordinary vegetative growth and mitotic division. In a broad sense this may be true, but it is doubtful if such a fine distinction can be drawn as to suppose that vegetative growth in the ovules can go on normally in a flower which is *apparently* unable to proceed with the reduction process in the anthers. Circumstantial evidence of the inability of the pollen mother cells to undergo meiosis is afforded by *Saxifraga* and *Ranunculus*, and further evidence of the strain imposed on the organisation of the flower by the meiotic process is supplied by *Aesculus* and *Asparagus*. In the flowers of *Aesculus*, both male and female organs have reached the same point of development simultaneously; the metabolism rate, this term being used in a broad sense, may be assumed to rise preparatory to reduction divisions in both anthers and ovules. In the lower regions of the inflorescence, sufficient supplies are available for the "peak loads" of both sets of reproductive organs, but in the upper regions the suitable supplies are reduced.

(The terms "upper" and "lower regions" are used to indicate an arbitrary division. The distinction between male and hermaphrodite regions is not rigid, examples of both floral types being found in both regions.) Again in the upper regions of the inflorescence, both male and female organs are waiting for the increase in energy supply, but in the anthers, with an assumed advantage in vascular supply at the moment, it is felt earlier. The reduction divisions in the pollen mother cells commence, causing such a demand that all the supplies to the flower are immediately diverted through the anther bundles. In short, in the lower regions there are sufficient supplies for both organs to commence and continue development, but in the upper the reduced supplies have introduced the competitive influence between the parts concerned, with subsequent development of those parts in the more advantageous position, viz. the anthers. The sudden collapse of the somatic nuclei in the ovules of *Aesculus* is good evidence of this, and a similar interpretation might be applied to the ovule-deficient *Asparagus*.

This possession of a larger or more suitable supply of nutriment through the vascular tissue at the critical moment when both anthers and ovules are ready to enter meiotic prophase is regarded as the main factor in deciding the type of floral deficiency or "sex" that arises in a given species. It is this factor which might explain the known occurrence of only one ovule-deficient plant in *Ranunculus acris*. The possibility that the stamens would be able to divert the main stream through their bundles at the critical moment is remote, from the very nature of the vascular structure of the floral receptacle. The writer does not agree with the suggestion made in the paper on the genetics of *R. acris* (Marsden-Jones and Turrill, 1929) that "it is possible that, owing to the marked self-sterility occurring in *R. acris* and *R. bulbosus*, and the consequent uselessness of 'own' pollen to a plant, there is a tendency to sex segregation as a degree of a division of labour...some plants specialising in femaleness, others remaining hermaphrodite or even, rarely, becoming male....It may even happen that populations will eventually become dioecious." The Buttercup types should probably be regarded rather as examples of physiologically deficient plants, handicapped from the early stages of development by the inability to form male gametes normally. The matter is probably not one of genetic relationship, for anther-deficient types can apparently arise both in intra-specific crosses in *Ranunculus* and in inter-specific crosses between two distantly related species of *Saxifraga*. Nor does self-sterility appear to have much connection with the problem for, although *Ranunculus* is

self-sterile, *Silene* and *Saxifraga* are quite self-fertile, but nevertheless produce deficient plants.

It is also difficult to see how, if the change to a unisexual state is considered to be progressing, a "dioecious population" could arise in such a plant as *Ranunculus*. At the present rate of progress, the overwhelming bias towards "femaleness," a trend which has been suggested as natural from the floral morphology, means that in the ultimate dioecious population, "male" plants would be extremely rare. It is probable that the species would have to resort to some apogamous method of reproduction if it were to continue in existence.

To return to *Asparagus*, the vascular supply which passes out to the two important parts of the flower is apparently so equal that it is only some slight difference, either in the quality of the bundles of one plant compared with another, or in the comparative distance of the sporogenous tissues from the point of separation of both stamen and ovary bundles, that decides which tissue shall gain the ascendancy. The fact that one species always produces deficient flowers of one type, and that a species of a different genus may produce flowers of quite a different but equally constant type, is regarded as evidence that there is something in the nature of the structure of the floral types which governs the nature of the deficiency met with. In the examples of floral deficiency studied in this paper, the greatest variety of abnormal types have been found, no one genus agreeing with any other. This is surely because we are studying as many different types of floral vascular anatomy, each responding differently to competitive influence. Hence, it would appear that plants with flowers of one or other of the deficient types are in a lower physiological category than the corresponding hermaphrodite types.

(3) *Interpretation of deficient types in* S. potternensis.

The application of the hypothesis of competitive development to the *Saxifraga* problem has tended to elucidate certain difficulties. In the first place, the anther-deficient types receive the same explanation as similar examples described earlier. The plant has been unable to supply sufficient suitable food material to the tapetum when it should normally become active and nourish the pollen mother cells during meiosis, but the vegetative development in the ovules has proceeded without interruption. A larger vascular supply to the ovary results; later it is seen that both the pollen mother cells and the archesporial cells in the ovules are approaching meiotic prophase. But the ovules, with the better

vascular system, will receive the "peak load" first, and will divert all nutriment through their bundles. The anthers may receive sufficient supplies temporarily, because of the increase to the flower as a whole, but ultimately this fails, with subsequent anther degeneration.

In explanation of the petal and ovule-deficient types, the plants are again assumed to be in a lower state physiologically than the typical hermaphrodite. The anthers have attracted sufficient nutriment for the commencement of reduction; they then divert such a quantity of supplies through their bundles that the vegetative development of the ovary is checked. The cells of the placenta lose their meristematic qualities to a great extent, sometimes entirely. If, however, the anthers complete pollen formation, the supplies will be available once more to the ovary bundles. If these are not already choked with gum, that part of the placental region which has not yet lost its meristematic powers through long starvation may commence growth, giving rise to the deformed ovaries noted in the description of B 2 F_1 Plant 3 (cf. p. 104). In commencing development so late, the young ovules are, however, diverting through the ovary bundles supplies which would normally have passed, at that stage of floral development, through the corolla bundles to the developing petals. Thus these are in their turn deprived of nutriment at the critical time, growth is arrested and the meristematic tissue loses its power of ever resuming active mitotic divisions (cf. *Silene maritima*, p. 109).

(4) *Seed production in* B 2 F_1 *Plant* 3.

As a result of the close correlation between anther, ovule and petal development, it is sometimes possible to forecast the quality and quantity of the seed production in certain of the deficient types in *Saxifraga potternensis*. Anther-deficient flowers when selfed give little seed, but when crossed with other pollen give abundant seed of good quality. Seed production in a plant with the simple petal deficiency is generally poor. A plant producing among its flowers petal-deficient types (B 2 F_1 Plant 3) as a rule also produces flowers with petals that approach normality, and there is probably some correlation between petal development and seed production in such a plant. Flowers with poor petals should show some seed, while flowers with good petals should produce little or no seed. This follows from the microscopical evidence, in which it was shown that in some cases ovule development was eliminated entirely (by assumed competition with the anthers). Such flowers should then be able to proceed with the petal expansion phase, which would

otherwise be interrupted by a delayed ovule development. This correlation between the two phases does not always hold in the *Saxifraga* plants owing to the introduction of petal metamorphosis at an early stage. It has already been stated that a metamorphosed petal does not affect ovule growth in the same way, and cannot, therefore, show any effect on seed production.

(5) *Dividing and resting periods.*

It was inferred earlier (cf. p. 101) that some influence causes the nucleus of the pollen mother cell to undergo division at the heterotype. In this connection we must regard the tapetum as the source of a driving force or energy, and the sporogenous tissue as a group of cells depending entirely upon the tapetum for the impulse to assume an active condition, that is, to divide at meiosis. It is probable that the passage of the pollen mother cells through prophase is conditioned by the degree of activity of the tapetum. It is frequently observed in accounts of meiotic prophase that the tapetal cells become very active at this stage; the nuclei show marked staining powers, the nucleolus generally subdivides and large vacuoles may appear in the cytoplasm. The tapetum may, in fact, be described as the intermediary between the sporogenous tissue and the organisation of the plant; it elaborates the food materials coming through the staminal bundles, and supplies energy in the form of nutriment to the developing mother cells. But such energy is not regular in supply. We may assume that it reaches a "peak" during the time of greatest activity, from diakinesis to heterotype telophase, that it falls temporarily causing the inactive "resting" stage of interkinesis, and that it rises again to enable the pollen mother cells to complete the homotype division. Such may be the normal course of events in a *Saxifraga* plant, but in the F_1 plants studied it is evident that the necessary energy is not regularly available to all cells in an anther loculus. Thus certain nuclei undergoing the first division of meiosis may experience considerable difficulty in the separation and subsequent passage of their chromosomes to the poles. All grades from the normal type of interkinetic nuclei to the "reconstituted nuclei" may therefore be found. The stage of division reached when the "resting influence" or the reduction in supply of energy occurs, depends upon the amount of energy that was available to any particular cell for the reduction process.

IX. Summary.

The tetraploid *Saxifraga potternensis* has arisen as the result of semi-heterotypic divisions at meiosis in the F_1 generation of the cross, *S. rosacea* by *S. granulata*. The semi-heterotypic divisions are found to be due to unequal distribution of energy or nutriment from the tapetum to the pollen mother cells. Those nuclei which have just commenced division when the "resting period" (interkinesis) begins become reconstituted within a single membrane, thereby cancelling reduction.

The problem stressed in this paper is the origin of the "deficient" forms of floral morphology. Detailed comparisons with aberrant forms from other genera leads to the conclusion that they arise as the result of competitive development, one floral part becoming "deficient" through "competition" with another.

The factor which introduces this competitive influence is conceivably a reduced nutrition level in flowers; a subsidiary factor is the high metabolism rate necessary for meiosis. Thus, in *Aesculus*, the "male" flowers in the upper regions of the inflorescence arise as a result of the elimination of part of the ovule development phase by the anther phase, following competition for the reduced food supply in that region. The morphology of the flower is an important factor in governing the type of deficiency to be found subsequent to such competition. The great variety in the types of deficiency studied is correlated with a similar variation in floral structure. Upon the introduction of competition, each type of flower studied has reacted in a different manner.

We thus reach the conclusion that every flower has a definite sequence of developmental phases, for the complete and normal development of which a certain optimum metabolism rate in anthers and ovules is the most important factor. Any decrease in the nutrition level of such flowers may affect, directly or indirectly, one or other of the developmental phases, and anther or ovule deficiency, producing sterility, or petal deficiency, producing abnormal floral types, are found.

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A NEW HAPLOID *OENOTHERA*, WITH SOME CONSIDERATIONS ON HAPLOIDY IN PLANTS AND ANIMALS.

By Prof. R. RUGGLES GATES and Miss K. M. GOODWIN.

(With One Plate and Four Text-figures.)

In 1929, a single plant survived to maturity in a culture of non-viable F_1 hybrids resulting from *Oe. rubricalyx* pollinated by *Oe. eriensis*. It was dwarfed in the size of all its parts, as well as completely sterile, and was finally suspected of being a haploid mutant. Subsequent cytological examination has shown this to be the case. A short note has already been published on the subject (Gates, 1929). Having observed this haploid, the senior author believes that certain small aberrant plants, not of the usual dwarf types, which have occasionally occurred in his cultures in earlier years, were also haploid in nature. It is desirable that geneticists should keep in mind the possibility of the occurrence of such haploid sterile small plants in their cultures, for they are probably of more frequent occurrence than has hitherto been supposed. The sterility of such plants is in some cases more conspicuous than their smallness of size.

Occurrence of haploid *Oenothera rubricalyx*.

In 1927, reciprocal crosses were made between *Oenothera rubricalyx* and *Oe. eriensis*, both of which have fourteen chromosomes. *Oe. eriensis* × *rubricalyx* gave a uniform F_1 with the red pigmentation characteristic of *rubricalyx* and the small flowers of *eriensis*. In several other characters they were patroclinous. This cross, which has been made three times (84 plants), is illustrated by Plate VII, figs. 1 and 2. Photographs of the parent forms can be seen: of *Oe. rubricalyx* in Gates (1914), Text-figs. 8–10 and of *Oe. eriensis* in Gates (1927), Text-figs. 5–7.

The reciprocal cross, *rubricalyx* × *eriensis*, made at the same time, produced seedlings which, although they germinated promptly, were yellowish in colour, developed very little chlorophyll and died in about 2 weeks, immediately their store of nourishment had been exhausted. This cross was made twice in 1927 and twice in 1928, the seeds from each cross being sown in the following year. The four F_1 families, from separate plants in each case, numbered respectively 36, 4, 21 and 85

seedlings (total 146). All four families consisted of small, feeble seedlings which died off simultaneously, showing the lethal effect of the cross. The largest family, grown in 1929, numbered 85 seedlings, 2 of which survived for 3 months. One of these died and the other lived long enough to be planted out in the culture bed. It reached maturity and belonged to a new type, very much dwarfed and almost completely sterile as regards pollen and seed production. This was the haploid.

Description of haploid.

The rosette was very small, with very narrow leaves, which might be supposed to resemble those of *eriensis* in shape, but with the red midrib colouring of *rubricalyx*. Plate VII, fig. 3, is from a photograph taken when the stem was beginning to develop, and fig. 4 shows the plant in flower. Several bags are attached to the stem, as numerous unsuccessful attempts were made to obtain seeds from it by selfing and crossing. The leaves of this plant were very narrow and pointed, only slightly crinkled, the midrib and petiole red above and below, as in *rubricalyx*. The stem, ovary, hypanthium and sepals also showed the characteristic red. The flowers were smaller than in *rubricalyx*, but unfortunately the petals were not measured, since the special interest of the plant was not recognised until later. Throughout the flowering season as the flowers opened the petals remained crumpled, as in a newly opened bud, never becoming stiff and smooth as normally. This was partly because of their thinner texture.

The pollen, on examination, was seen to consist mostly of shrivelled grains, but no estimation was made of the proportion of apparently good pollen. The anthers were deformed, twisted, and yellowish brown rather than bright yellow in colour. Not only were all attempts to obtain seeds from the numerous flowers unsuccessful, but open pollination gave twisted poorly developed, shrivelled capsules. Most of the ovaries fell off before any seed was set, but the capsules resulting from open pollination showed the presence of a few small seeds, varying in number from 1 to 6 in a capsule. Attempts were made to germinate these seeds, but without success.

The whole appearance of this plant suggests that it was a miniature *rubricalyx*, although in the early stages of its development the narrow and pointed leaves were interpreted as resemblances to *eriensis*. Since it proved to have 7 chromosomes, it presumably came from the development of a haploid *rubricalyx* egg cell without fertilisation, the presence of the foreign *eriensis* pollen tubes presumably acting as

stimulus. The non-viable seedlings from this cross were probably true diploid hybrids, but there has been no opportunity to count their chromosomes.

In crosses, *Oe. Lamarckiana* produces the well-known twin types *laeta* (with broad, darker green leaves, etc.) and *velutina* (narrow-leaved) and is, therefore, regarded as made up of the two complexes, *gaudens* and *velans*, the homozygous recombinations *gaudens . gaudens* and *velans.velans* being non-viable. That being the case, it is possible that *Oe. Lamarckiana* cannot produce a viable haploid *gaudens* or *velans*. *Oe. rubrinervis* is similarly regarded as *deserens.velans* by de Vries and as *subvelans.paenevelans* by Renner (1918), *subvelans* corresponding to *gaudens*. *Oe. rubricalyx* differs from *rubrinervis* only in a dominant gene mutation, both forms having the same chromosome linkage, four pairs and a ring of six.

Probably both the surviving seedlings in the 1929 culture from *Oe. rubricalyx* × *eriensis* were haploids, and as one was larger, stronger and healthier than the other, it is possible that one represented the haploid *subvelans* and the other *paenevelans*. The narrow leaves of the haploid which reached maturity might lead one to identify it as *paenevelans*, but the haploids frequently have narrower leaves than their diploid counterparts, and as the other seedling was smaller and weaker it might represent *paenevelans* and the surviving haploid be *subvelans*.

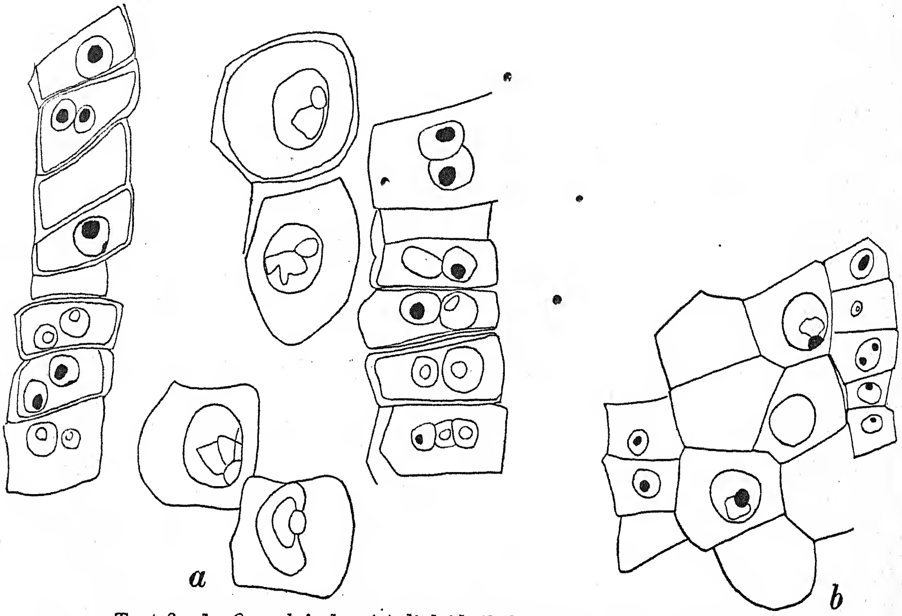
On the other hand, the *velans* complex contains the tendency to reddish sepals, and it appears most likely that the dominant gene for *rubricalyx* bud-coloration arose in this complex. Hoeppener and Renner (1929) suggest the term *pervelans* for this altered complex.

Cytological observations.

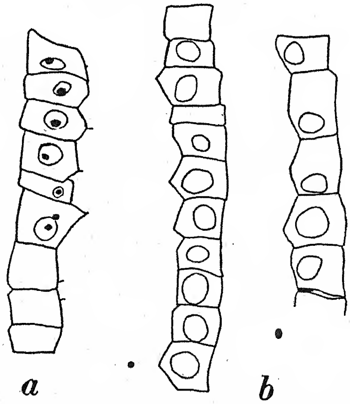
Two collections of cytological material were made from this plant by Mr D. G. Catcheside. Allen's modification of Bouin's fixative was used in one case, and Kihara's method of dipping into Carnoy before Allen's Bouin in the second. Sections were cut at 8–10 μ and stained with Heidenhain. Unfortunately the material did not show stages later than synapsis in the pollen mother cells, so the behaviour of the chromosomes in diakinesis and the meiotic divisions has not been seen.

The pollen mother cells of a loculus are sometimes in two vertically seriated rows, but generally there is only one (see Text-fig. 1). The resting nucleus is followed by early heterotypic prophase, in which the nucleolus passes to the periphery of the nuclear cavity, the fine network of the nucleus becomes coarser, and the threads are seen to be made

up of a series of dark-staining granules on a finer filament. Larger aggregations of chromatin are constantly present towards the periphery. The nucleolus soon changes in shape from spherical to lensiform, and



Text-fig. 1. *Oe. rubricalyx*, (*a*) diploid, (*b*) haploid: pollen mother cells and tapetum during synizesis.



Text-fig. 2. Cells from petal epidermis of (*a*) haploid, (*b*) diploid *rubricalyx*.

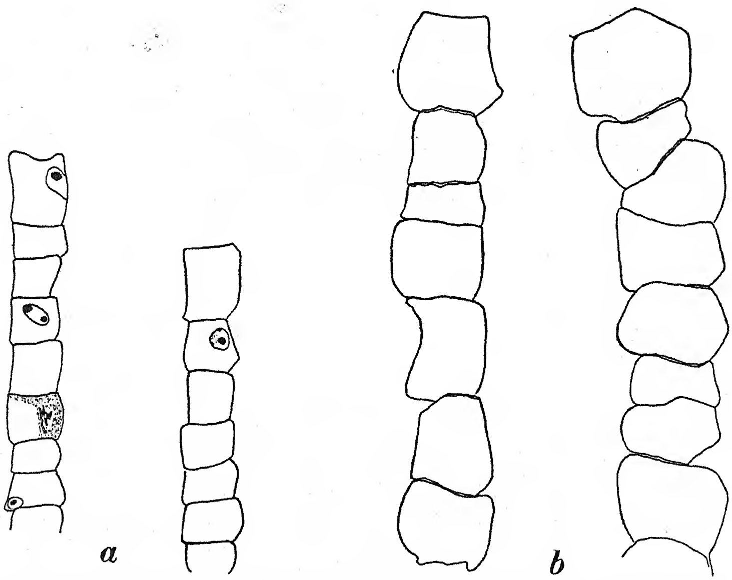
remains for some time pressed up against the nuclear membrane. In organic connection with it is the spireme, attached to the nucleolar body, which can always be seen when the nucleolus is sufficiently de-

stained. The nucleolar body does not project from the surface, but occasionally it appears to have spread over part of the surface of the nucleolus. The spireme is then attached to it at more than one point. Irregular chromatin aggregations appear in the meshes of the spireme.

Examination of mitosis in somatic tissues showed seven chromosomes (Plate VII, fig. 5). Counts were made from polar views of metaphase plates in petal cells, wall cells of the young anther, and occasionally in stigma cells.

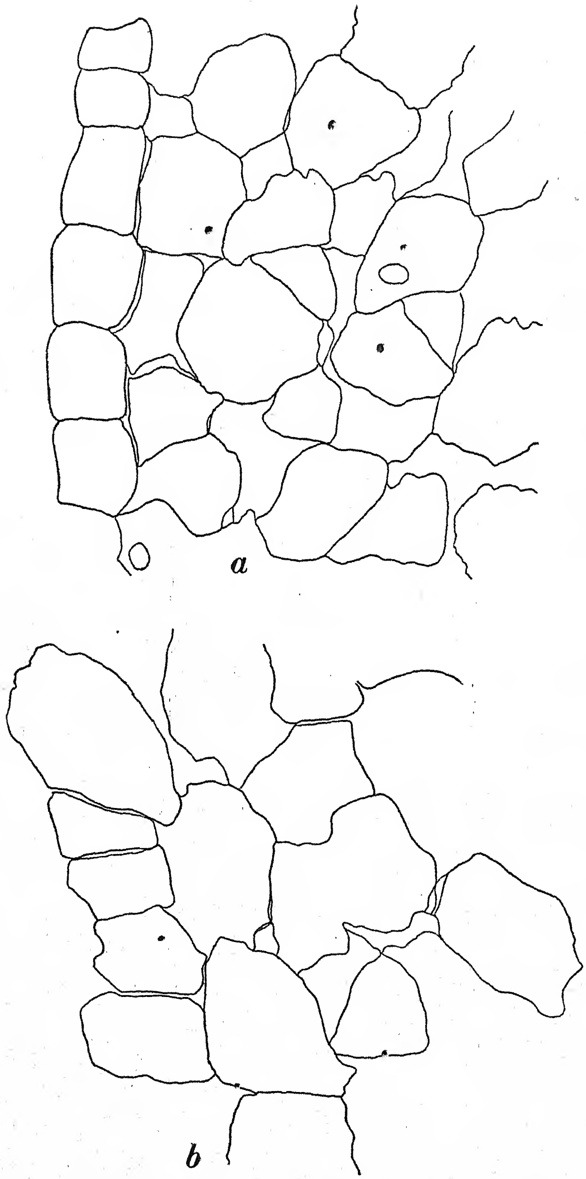
Cell measurements.

The haploid plant was conspicuously smaller than normal diploids, and this afforded an opportunity of determining the relation between



Text-fig. 3. Cells from anther epidermis of (*a*) haploid, (*b*) diploid *rubricalyx*.

cell size and plant size. Comparisons of cell size formerly made between *Oe. Lamarckiana* and its tetraploid mutation, *gigas* (Gates, 1909), showed that the ratio of increase of cell size varied from tissue to tissue. Similar series of measurements have been made of the tissues of *Oe. rubricalyx* and the haploid. These include pollen mother cells, their nuclei and nucleoli (Text-fig. 1), petal epidermis (Text-fig. 2), anther epidermis (Text-fig. 3) and stigma cells (Text-fig. 4) in the buds of the diploid and the haploid. The measurements of diploid *rubricalyx* were taken from preparations made by Dr F. M. L. Sheffield (Sheffield, 1927). Since



Text-fig. 4. Cells from stigma of (*a*) haploid, (*b*) diploid *rubricalyx*.

the resting stage of the nuclei in the pollen mother cells was not available in the diploid, the stages of synizesis were used for comparison, and the other tissue measurements were taken from buds of the same age.

The results are recorded in Tables I and II, but before considering them a few words are necessary regarding the methods of cell measurement adopted. The cells to be measured were drawn in outline at table

TABLE I.

Relative volume of cells.

	Oe. rubricalyx Haploid : Diploid	*Oe. Lamarck.* : *Oe. gigas* Diploid : Tetraploid	*Oe. rubricalyx* Diploid : Haploid
Petal cells (epidermal)	1 : 2·3	1 : 1·96	1 : 0·43
Anther cells (epidermal)	1 : 3·5	1 : 3·8	1 : 0·28
Stigma cells	1 : 2·3	1 : 3·1	1 : 0·43
Pollen mother cells (synapsis)	1 : 2·1	1 : 1·5	1 : 0·47
Nucleus in synapsis	1 : 3·2	1 : 2·16	1 : 0·31
Nucleolus (synapsis)	1 : 1·7	—	1 : 0·59
Synaptic "knot"	1 : 2·35	—	1 : 0·43
Tapetum cells (at synapsis)	1 : 2·7	1 : 1·44	1 : 0·37

TABLE II.

Cell measurements in μ.

	Haploid "Resting nuclear" stage			Diploid At synapsis		
	No. of measurements	Mean length	Mean width	No. of measurements	Mean length	Mean width
Petal cells (epidermal)	100	6·14	9·6	100	8·3	12·0
Anther cells (epidermal)	70	9·6	10·5	93	16·2	13·3
Stigma cells	70	21·9	15·7	50	28·0	21·9
Pollen mother cells	80	18·4	13·1	—	—	—
Nucleus	66	7·0	6·1	—	—	—
Nucleolus	64	2·6	2·6	—	—	—
Tapetal cells	54	7·9	11·1	—	—	—
	At synapsis					
Pollen mother cells	56	23·6	18·4	40	29·8	24·0
Nucleus	56	9·6	8·7	40	13·0	10·1
Nucleolus	56	3·4	2·4	40	4·3	2·6
Synaptic "knot" (surface area)	53	4·4	3·4	40	5·7	4·8
Tapetal cells	32	7·4	13·5	50	10·5	18·4

level by means of a camera lucida. A Spencer binocular microscope used as monocular with a $\frac{1}{12}$ in. oil immersion objective and a Zeiss $K \times 6$ ocular was used, giving a magnification of about 1150 diameters. The projected outlines were measured in mm., and the means recorded in mm. In calculating volumes, the pollen mother cells, nuclei and the stigma

cells were treated as spheres. The cells of the other tissues were assumed to be rectangular solids. Since the pollen mother cells are polygonal to roughly circular in outline, the greatest diameter was measured together with the diameter at right angles to it, the mean of the two being taken as the diameter of the sphere in calculating the volume. The nucleolus presented greater difficulty on account of its flattened lensiform shape during synizesis, but the mean of the longest and shortest diameters (which are at right angles to each other) was taken to represent the diameter of a sphere of the same volume. The synaptic "knot" during synizesis forms a roughly spherical mass, which has been treated as a sphere although a certain amount of inaccuracy is doubtless involved.

In measuring the somatic cells which are approximately rectangular in surface view, *i.e.* the petal epidermis, anther epidermis and tapetum, from flower buds collected at the time of meiosis, the cell measurement along the long axis of the petal or anther was regarded as its "length," and the measurement along the thickness of the organ as its "width." In calculating the mean cell volume, the lesser of the two measurements was taken as the third dimension in each case. "Length" treated in this way is frequently less than "width." Thus in the case of the petal epidermis, the mean dimension (7) measured parallel to the surface of the petal as seen in longitudinal section is less than the mean "width" (11) measured perpendicular to the surface of the petal. The mean volume was then taken as $7^2 \times 11$, since in surface view the epidermal cells are approximately iso-diametric. Epidermal cells are of relatively uniform "width" but vary greatly in "length," since they grow mainly and divide only in a plane at right angles to the surface. But the majority of measurements, even in this dimension, gave very steady and even results. These methods are essentially the same as were used in an early paper (Gates, 1909) in which the cell sizes of diploid and tetraploid *Oenothera* were compared.

Examination of Table I shows many interesting relationships. In every tissue examined, the cells are smaller in the haploid than in the corresponding tissue of the diploid, but the amount of decrease in size varies for different tissues. The comparative cell volumes for haploid : diploid are given, together with the diploid : tetraploid ratios for *gigas* (taken from Gates, 1909) and also the diploid : haploid ratio in *rubricalyx*, to show the amount of decrease in cell size of the haploid. Comparing columns 2 and 3, it will be seen that the $n : 2n$ ratio is generally in quite good agreement with the $2n : 4n$ ratio. Thus as regards petal epidermis the ratio is in both cases near 2 : 1, while for the anther epidermis it is

for some unknown reason distinctly higher at about 3·5 : 1. In measurements of stigma cells the agreement is not so good, although in both cases the ratio is above 2 : 1. There are divergences in the other tissues, but whether these are significant could only be determined by a larger series of measurements and perhaps greater refinements in the methods. It is significant that the size of the nucleolus and the area occupied by the spireme in synizesis are conspicuously smaller in the haploid, the decrease being in much the same ratio as for cell size. The spireme is presumably shorter, being composed of fewer chromosomes.

In the tapetum the ratio is less, the cells of the haploid being notably small and less deep-staining than in the diploid, probably due to lack of nutrition. The pollen mother cells also fail to separate and round off at synizesis as they do in diploid *rubricalyx* and generally in other forms. In *Oe. gigas*, however (Gates, 1911), flowers were found in which the pollen mother cells failed to separate even after the tetrad divisions were completed. This is probably due partly to insufficient room owing to lack of growth of the wall layers; and partly to low osmotic pressure within the cells.

The actual cell measurements of the haploid and diploid in μ are given in Table II. The mean diameter of the pollen mother cell nucleus at synizesis is $9{\cdot}15\,\mu$ in the haploid and $11{\cdot}5\,\mu$ in the diploid. Comparison of longitudinal sections of the anthers shows interesting differences between the haploid and diploid in morphological detail. These are set forth in Table III.

TABLE III.

	Haploid	No. of measurements	Diploid	No. of measurements
No. of pollen mother cells in median longitudinal sections of anther	40	30	48	37
No. of cell layers in anther wall	4*	32	4†	52
Width of loculus of anther	32	25	55	25

* A few with five layers, cells very narrow.
† A few with three layers, cells larger and broader.

Thus, although the pollen mother cells are smaller in the haploid, yet the number of such cells is larger in the diploid. Again, both types of anthers usually have four wall layers; yet there are occasionally five in the haploid and three in the diploid. Hence the haploid does not correspond cell for cell with the diploid. The same was true of the tetraploid (Gates, 1909). As regards chromosome size, a few measurements of the somatic chromosomes in dividing anther and petal cells of both haploid and diploid failed to reveal any appreciable difference in size.

RECORDS OF HAPLOIDY IN FLOWERING PLANTS.

Records of haploidy are as yet uncommon in seed plants, and in animals they are still rarer, although in certain animal species haploidy is the normal condition of the males. The first haploid seed plant was described by Blakeslee, Belling, Farnham and Bergner (1922). Two such plants appeared in the offspring of normal *Datura* plants, which had been subjected to low temperature at about the time of fertilisation in an attempt to produce chromosomal irregularities. It was supposed that the low temperature acted as a stimulus in causing the parthenogenetic development of two egg cells. If that is the case, it may be expected that late seeds with haploid embryos will be found among species of wild or cultivated plants growing in climates with autumnal frosts followed by warm weather. The relative weakness of such plants and their failure to propagate themselves, together with their near resemblance to diploid plants except in sterility, would account for failure hitherto to note their occurrence in the floras of temperate regions. The haploids since recorded do not, however, show in their origin any special relation to temperature, and carefully controlled experiments are required before it can be determined whether such a relation exists. Belling and Blakeslee (1927) have also obtained haploid Daturas by pollinating *D. stramonium* with pollen of *D. ferox*. About 12 per cent. of good pollen grains are formed.

Although the haploids are almost completely sterile in ovules and pollen, occasional seeds result from self-pollination, which produce completely homozygous diploid plants. Up to the year 1927, over 50 haploid mutants of *Datura* had been identified (Blakeslee, Morrison and Avery, 1927). The original plant was kept in cultivation by grafts and cuttings, and produced 393 descendants from seeds. In this homozygous line have been obtained $3n$ and $4n$ individuals as well as the various trisomic $(2n + 1)$ types, the latter appearing with the high frequency of about 3 per cent. in the F_1 generation from selfing. Moreover, the haploid has produced twice, or probably four times, in the F_1 generation a plant heterozygous for a new gene mutation. Probably each occurred in a single egg or pollen grain of the haploid. The new recessive mutations are called "curled" (referring to the cotyledons) and "tricarpel." Their linkages show that they occurred in different chromosomes. An absolutely homozygous diploid line derived from a haploid does not therefore necessarily remain homozygous.

The chromosome arrangements in haploid, diploid, triploid and

tetraploid Daturas are compared by Belling and Blakeslee (1923). They found that in the pollen mother cells of the haploid the chromosomes are usually distributed by chance, $6 + 6$, $5 + 7$, $4 + 8$, etc., just as if their normal partners were present, producing small nuclei and diminutive pollen grains which perish. Later (1927) it was shown that all the chromosomes divide regularly in the homotypic, forming usually two larger and two smaller nuclei. One or more chromosomes may be detached in anaphase I and form extra microcytes. But frequently non-reduction occurs, the chromosomes dividing longitudinally and producing two pollen grains of normal size, each with 12 chromosomes. Non-reduction is much more frequent in the haploid than in the diploid or triploid, varying in frequency from 10 to 29 per cent. The authors also found that the volume of the pollen mother cells in n, $2n$, $3n$ and $4n$ plants was nearly proportional to the number of haploid groups of chromosomes present.

Belling and Blakeslee (1927) showed that the volume of the pollen mother cells in the haploid is about half that in the diploid, the relative diameters being 1 : 1·26, *i.e.* the linear dimensions are about 1/5 less than in the diploid. The organs of the haploid are reduced in somewhat similar ratio. This applies to the ovary, style, filaments, anthers, corolla and calyx; also to the leaves and the plant as a whole.

The next record of haploid seed plants was by Clausen and Mann (1924). One appeared in the F_1 (58 plants) of *Nicotiana Tabacum* var. *purpurea* × *N. sylvestris*. The cross gave a uniform, vigorous hybrid progeny which was almost completely sterile. The exceptional plant was a "reduced replica" of var. *purpurea*, but with its characters somewhat more pronounced. It was about three-quarters the height of normal *purpurea*, with smaller leaves and flowers and more slender stems. It bloomed freely but was completely sterile in pollen and seeds. This plant had 24 chromosomes, which is the haploid number for *N. Tabacum*, while *N. sylvestris* has $n = 12$. Another haploid plant appeared in F_1 (50 plants) of a fifth generation hybrid involving *N. Tabacum* var. *macrophylla*, which was pollinated by *N. sylvestris*. The bulk of the plants fell into two expected classes, while the haploid was a reduced replica of *macrophylla*. Chipman and Goodspeed (1927) have since made a cytological study of the *purpurea* haploid. They find a pairing of threads before synizesis in the diploid, but not in the haploid. In the latter a single spireme segments into the 24 chromosomes. These facts are apparently regarded as showing a parasynaptic pairing in *N. Tabacum*. It is also worth noting that the occurrence of synizesis in the haploid

shows that its significance cannot be to bring about pairing of the chromosomes, since bivalent chromosomes are not formed in the haploid. In this connection it is worth while recalling that synizesis has also been observed in tapetal cells of *Lactuca* (Gates and Rees, 1921) in which, of course, no reduction takes place.

Subsequently three more haploid *N. Tabacum* var. *purpurea* and two var. *Cuba* plants appeared and were studied by Ruttle (1928). Examination of root tips from cuttings of haploid plants showed that 52 were haploid, 22 diploid and 8 contained both haploid and diploid cells. The latter were always larger, but not so much so that every cell could be identified as haploid or diploid when not in division. The area of diploid cells in the latter roots varied from a small group of cells near the growing point to a large sector of irregular outline in the meristematic region. Diploid cells were not found in the archesporial tissue, pollen mother cells or ovules of the haploids, such cells being apparently confined to the roots.

A haplont occurring in a pure line of *N. glutinosa* has recently been described (Goodspeed and Avery, 1929). The plant was one of a culture which had been subjected to X-rays as seedlings, but its origin was spontaneous and unconnected with the treatment received. It was considerably reduced in size, and the flower colour was greenish yellow rather than salmon-red. The forms of leaf and flower were considerably altered, but anthers and ovaries were completely sterile. This plant continued to grow vigorously long after the diploid plants had ceased to flower. In pollen meiosis the 12 chromosomes were distributed at random. Not infrequently, a suspended anaphase was followed by an equation division, producing a pollen dyad. Such pollen grains should be functional.

Clausen and Lammerts (1929) have discovered a most interesting case of haploidy of another kind in *Nicotiana*. They crossed *N. digluta*, an allohexaploid with carmine flowers and 36 bivalent chromosomes, with the pollen of a form of *N. Tabacum*, identical with var. *purpurea* except in having white flowers. The latter had 24 bivalents. The F_1 (173 plants) included various plants with aberrant chromosome numbers, but a single plant with small white flowers was identical in its other features with haploid *purpurea*. It was completely sterile, had 24 univalent chromosomes in its pollen mother cells, and these were usually distributed at random. This plant thus agreed morphologically and cytologically with other haploid *Tabacum* plants. In one mother cell 19 of the univalent chromosomes were seen to divide, while the rest separated, one half-univalent being fragmented into two.

There seems no doubt that the origin of this plant is a case of androgenesis (Wilson, 1925) or haploid merogony[1], the male nucleus developing in the egg cytoplasm, but there is no indication as to how the egg nucleus was dispossessed. Probably like other plants in this series it had an irregular chromosome content, which may have been incomplete in the embryo sac nuclei following meiosis. When *N. digluta* originated, a form occurred which is now recognised as a *purpurea* haploid which must also have arisen merogonically. In the back-cross (*N. sylvestris* × *Tabacum*) × *sylvestris*, occasional plants have been known to appear which are identical with *N. sylvestris* in cytology and morphology. These are now regarded as probably due to diploid merogony. In such cases the male nucleus presumably entered the egg cytoplasm, the egg nucleus disappeared and the chromosome number was doubled shortly after this egg began its merogonous development. In no case was there any detectable influence of the maternal cytoplasm.

Kostoff (1929) has obtained a similar case by pollinating an aberrant plant of *Nicotiana Tabacum macrophylla* having 70–72 chromosomes with pollen from *N. Langsdorffii* ($n = 9$). An abundance of seeds were obtained which germinated easily, producing about 1000 seedlings, of which only one reached maturity. This was a haploid *Langsdorffii*, somewhat smaller than the diploid and having 9 *Langsdorffii* chromosomes. This androgenic haploid produced no seeds from selfing, but a few seeds by pollinating with diploid *Langsdorffii*. In the pollen mother cells of the haploid the 9 chromosomes do not form an equatorial plate, but spread out towards the poles of the spindle and separate at random ($4 + 5$, $3 + 6$, $2 + 7$, rarely $1 + 8$). Sometimes some of these chromosomes divide in the first division. When all the chromosomes remain in one group in interkinesis they all frequently divide in the second division, forming pollen dyads. But they may separate into two or more groups, each of which forms its own spindle, with resulting pollen triads, pentads or even octads. About 8 % of the pollen appears good, but the grains vary greatly in size. Of 58 root tips examined, all were haploid with an occasional diploid cell, except one which had $2n$ chromosomes. The volumes of the n and $2n$ cells were as 1 : 4.

Gaines and Aase (1926) obtained a "haploid" with 21 chromosomes by pollinating a winter wheat, *Triticum compactum humboldtii*, with the pollen of *Aegilops cylindrica*. Usually only shrivelled seeds result, but

[1] The first evidence of haploid merogony was obtained by Farmer and Williams (1898). They observed that in the brown alga Halidrys, enucleate fragments of egg cells were fertilized by sperms and formed a cell wall in the normal manner. But development was not seen to proceed further.

the single plump kernel which produced this plant was much larger than a normal seed of the *Triticum* parent. It is suggested that both male nuclei of *Aegilops* fused with the maternal endosperm nuclei to produce a giant (tetraploid) endosperm while the egg developed parthenogenetically. Gaines and Aase state that this "haploid" plant could not be distinguished until flowering time, when the spreading of the glumes, characteristic of sterility, drew attention to it. Their Text-figs. 1 and 2 (the legends of which have evidently been transposed) show that the hexaploid wheat has thicker stems and larger heads than the triploid plant. Also the pollen mother cells of the latter are distinctly smaller. It may also be mentioned as a peculiarity of the "haploid" plant that all the pollen mother cells of a loculus sometimes more or less completely coalesce, large spindles appearing which bear the chromosomes of several coalesced nuclei. In somatic tissues of the ovary giant cells were frequently found, with large nuclei formed by the fusion of pairs of somatic nuclei. Binucleate cells are known to be of widespread occurrence in young tissues of flowering plants, but here they are of exceptional frequency. The nuclei in somatic cells of the stamens and pistil of the haploid are stated to be smaller than in the parent with 42 chromosomes, but some large nuclei were found here with three or four sets of chromosomes. This frequent occurrence in the haploid of somatic cells with two fused nuclei corresponds with the fact that in parthenogenetic frogs the diploid chromosome number is restored during ontogeny. One other point concerning the haploid wheat plant is that its 21 chromosomes were distributed by chance in meiosis, without any evidence of pairing, although this point deserves further study. It therefore behaved as a haploid, and not as many triploids behave. We may conclude that this $3n$ wheat plant was actually smaller in the size of its organs, as well as in cell size, than the $6n$ parent.

Jørgensen (1928) obtained interesting results in producing haploid as well as diploid individuals like the female parent by pollinating *Solanum nigrum* with pollen from *S. luteum*, *S. aethiopicum* or other species which would barely cross, if at all, with *S. nigrum*. The pollen must germinate on the stigma and stimulate the parthenocarpic development of the fruit. Such fruits are small, and many drop before maturity. They contain few or no seeds, and such seeds as occur require special methods of germination. In all, from 90 such pollinations 43 fruits were obtained; about 70 seeds were prepared for germination, and 35 plants were reared from them. Of these, 28 were diploid and 7 haploid, all typical *S. nigrum*, and the diploids bred true.

Only once was a true hybrid between *S. nigrum* and *S. luteum* formed. In grafting experiments by Mr Crane at Merton, periclinal chimaeras were produced, some of which after selfing formed fruits with viable seeds. One such plant from seeds of *S. nigrum* var. *gracile* with a one-layered skin of *S. sisymbrifolium* was a haploid. Perhaps, as Jørgensen suggests, the germination of the *nigrum* pollen of the chimaera on the *sisymbrifolium* skin was delayed and some of the egg cells were meantime stimulated to form embryos. Apparently *S. nigrum* never produces haploid offspring when left to flower freely, but it might do so if only a few pollen grains were placed on the stigma, since their pollen tubes might then act as a stimulus to unfertilised eggs to develop.

Jørgensen has examined embryo sacs of *S. nigrum* from flowers pollinated by *S. luteum*. He finds that the male nucleus (sometimes both) enters the egg cell, but there disintegrates while the egg divides to form the embryo (gynogenesis). In some such embryos the mitotic divisions showed approximately the haploid chromosome number (36), in others the diploid (72). It was not discovered how or when the doubling in the latter case took place, but the first mitosis of the haploid egg was regarded as the most probable place. As regards external characters, the haploid *S. nigrum* seedlings have narrow cotyledons and form delicate and slender plants. They have rather long internodes, and being almost completely sterile they continue growth longer than the diploids. Their leaves are smaller and markedly narrower, with less dentation and a thin lamina. The pollen is nearly all shrivelled, the few living grains being nearly normal in size. Comparison of Jørgensen's figures indicates that the cells of the root tip and the pollen mother cells and their nuclei are smaller in the haploid than in the diploid.

The meiotic divisions of haploids were studied, both in the microspore and megaspore formation. In the former, the chromosome pairing approached the condition $12_{II} + 12_{I}$, as exhibited by many triploids. From this fact the conclusion is drawn that capacity for conjugation is not a reliable measure of the degree of identity between the chromosomes in a pair. In the megaspore mother cell "the number of univalents apparently does not exceed 12," but occasional trisomes occur and most of the univalents go to the upper pole, so that unequal divisions, such as 20 + 16, occur.

Noguchi (1928) has described in *Brassica* a case of pseudogamy similar to that of Jørgensen in *Solanum*. When *B. campestris* var. *oleifera* is pollinated from *B. oleracea* var. *gemmifera*, the pollen tubes enter the embryo sac but the male nuclei do not fuse with the egg or the polar

nuclei. They shortly disintegrate, but the egg is stimulated to develop by the entrance into it of a male nucleus, and an embryo is formed.

In some *Matthiola* hybrids, Lesley and Frost (1928) obtained in F_2 two extreme dwarfs, one of which was diploid (14 chromosomes) with two extra chromosome fragments, the other haploid with one such fragment. The pollen mother cells of the haploid had about half the volume of those in diploids. Pollen dyads were frequently formed, the cells of which were of about the same size as the cells in a pollen tetrad of the diploid. In some cases there is random segregation of the haploid chromosomes, followed by other irregularities. But frequently the chromosomes split and separate (except sometimes the extra fragment), the heterotypic mitosis evidently being omitted. This results in a pollen dyad. The seven chromosomes plus a fragment were also seen in somatic cells from young buds.

Among a progeny of 1700 F_1 hybrids of *Crepis capillaris* × *C. tectorum*, Hollingshead (1928) has described two haploid individuals of *C. capillaris* ($n = 3$). The records show that the prevailing temperatures were low at the time of making these crosses, the minimum occurring on the night following the cross which gave rise to the two haploids. It is therefore uncertain whether cold or foreign pollen is the exciting cause in this case. The haploids were much smaller than normal, with shorter and narrower leaves. Root tips were examined and the cells found to be smaller, but each was recognisable by its characteristic morphology. Diploid tissue was found in the roots of one plant, one root showing only diploid cell plates, another a small diploid area in the central cylinder, and a third a small area in the outer cortex.

M. Navashin (1927) found in the F_2 progeny (three plants) from *Crepis tectorum* × *C. alpina* a diploid *alpina* plant, but this was probably a case of segregation and not of merogony.

A haploid tomato mutant with 12 chromosomes has been described by Lindstrom (1929). It appeared in the F_2 numbering 337 plants, of a varietal cross showing complete fertility, and may therefore be regarded as "spontaneous." Its parents carried factors for dwarfness, and smooth, ovate fruit. Five generations of cuttings, numbering about 300 individuals, have been derived from it. The stature of the haploid is that of the dwarf types, and it has been shown to be genetically a dwarf, but it has much smaller leaves and distinctly smaller flowers. Although nearly sterile, 42 plants have been obtained by using the pollen of other varieties. Three plants have been obtained from open-pollination, and these are believed to represent actually self-pollinations, very small

fruits being formed. These plants are diploid dwarfs. Root tips of the haploid show occasional diploid cells. Nevertheless in all the numerous cuttings the haploid phenotype has persisted, and Lindstrom has failed to get a diploid plant from them. This striking vegetative stability of the haploid tomato is in contrast with the *Datura* and *Nicotiana* haploids. In the pollen mother cells irregular random separation of the 12 chromosomes takes place.

In the light of these cases, the results of Collins and Kempton (1916) can be interpreted. From *Tripsacum dactyloides* × *Euchlaena mexicana* they obtained 4 seeds and a single F_1 seedling which was like the male parent. It remained true in the F_2 (3 plants) and the F_3 (10 plants) and was regarded as a case of false hybridization or "patrogenesis." No cytological studies have been published, but this was probably a case of androgenesis, the plant becoming diploid either in the F_1 or F_2 generations. *Tripsacum* × *Zea* also produced a few seeds. The F_1 plants were *Tripsacum*, so this was probably a case of parthenogenesis induced by the maize-pollen, but whether these plants were haploid or diploid is unknown.

The cytology of hybrids from *Nolana prostrata* × *N. atriplicifolia* was studied by R. O. Whyte (1929). Both these species have 12 chromosomes as haploid number, but the F_1 plants with 24 chromosomes show only three or four bivalents in heterotypic metaphase, and produce only 5–10 per cent. of good pollen. The plants examined in F_2 and later generations, however, showed greater regularity in meiosis, 10 or more bivalents occurring regularly, and about 50 per cent. of good pollen being produced. One bud collected from an F_3 plant which was regarded as typical of its generation was believed to be haploid. The evidence is not very satisfactory, as the chromosome number could not be accurately counted, but a figure is given which bears some resemblance to the "reduction" division in the pollen mother cells of haploids, and this appeared to be confirmed by the examination of somatic plates in the stylar tissue. This plant had previously given seed which produced a normal F_4, so it is regarded as probably a diploid plant which developed a haploid shoot late in the season.

Very recently Davis and Kulkarni (1930) have published an account of haploid mutations in *Oe. franciscana*. The type first appeared in 1923 and was called "pointed tips." Such plants are of about half the stature of *franciscana*, and all their organs are proportionately smaller. The leaves are narrower, sharply pointed, and the bud cones more attenuate. The flowers are about half as large as in the diploid, and pollen is developed

only in small amounts, the grains being mostly shrunken. A few seeds are developed from selfing. This haploid has appeared "spontaneously" four times in several generations, with a frequency of about 1 in 1000. It has also occurred in crosses of *franciscana* with certain of its derivatives. When selfed, the haploid produces diploid plants, but a few haploids appear, indicating that the haploid egg can again develop parthenogenetically. Two new mutant types also appeared, as well as other aberrant individuals. The haploid crossed with diploid pollen gave ordinary *franciscana* as expected. A completely sterile haploid of *Oe. Hookeri* also appeared among 1291 plants, suggesting the same frequency of parthenogenesis as in *franciscana*.

In the cytological account of these haploids, it was found that the spireme segments into seven chromosomes which do not pair. The mass of sterile pollen results from irregular distribution of the chromosomes in the heterotypic mitosis (6 + 1), (5 + 2), (4 + 3). In those cases which lead to functional pollen grains, the multipolar spindle is stated to become unipolar, the seven chromosomes all becoming attached to spindle fibres from that pole. The heterotypic mitosis being omitted, the nucleus is reconstituted and the chromosomes split. This corresponds with the period of interkinesis, and is followed by an ordinary homotypic mitosis in which seven chromosomes pass to each pole of the spindle and a dyad of pollen grains is formed. It is worth noting that sometimes a small enucleate mass of cytoplasm is separated off from these cells. The homotypic spindle may (rarely) also be unipolar, with the result that the seven split chromosomes reconstitute a single nucleus, and a single giant pollen grain whose nucleus contains 14 chromosomes will be formed. One such case was observed, a small mass of cytoplasm without a nucleus being separated off at one side of the cell. The formation of a dyad of full-sized pollen grains by omission of the reduction division confirms the observations of Belling and Blakeslee (1923) on haploid *Datura*.

It may be remarked parenthetically that Metz (1926) has described in four species of the Dipteran genus *Sciara* a monocentric or unipolar spindle in the first meiotic division in spermatogenesis. The chromosomes consist of four pairs, and two others which make up the *X*. All are attached to spindle fibres from the single pole. Nevertheless, one of each pair, together with the two composing the *X*, pass towards the pole, while the remaining four diverge at first in the opposite direction but finally converge at a point where the other pole would be expected to exist.

Still more recently, in a number of *La Cellule* which appears to have

been actually published about 30 March 1930, Emerson (1929) gives an interesting independent account of the pollen meiosis in haploid *Oe. franciscana* which is surprisingly different in some respects from that of Davis and Kulkarni. Emerson's haploid appeared in an F_1 of 461 plants grown at the University of Michigan, from *Oe. franciscana* crossed with the hybrid known as *franciscana sulfurea*. The atypical plant had extremely narrow leaves in the rosette stage and was a weak semi-dwarf, almost completely sterile. It is stated that the spireme in the pollen mother cells is not continuous, and parallelisms of threads are found to be quite as numerous during synapsis as in the diploid. Later, the spireme in many nuclei appears continuous. It is thrown into loops, the arms of which are twisted about each other. It is concluded that since this twisting occurs in the haploid, it cannot be the basis of genetical crossing over.

A second contraction stage occurs, followed by segmentation of the now heavy thread. The seven chromosomes are probably all end-to-end in this spireme, but only a case with four attached tandem-wise is actually shown. Later, the chromosomes are all separate, but in many of the cells two are attached end-to-end. There is some evidence that this pair behaves differently from the five univalents. In heterotypic metaphase they remain frequently, and perhaps always, attached. This pair is less condensed than the others, which are nearly spherical. In early anaphase the members of the pair usually pass to opposite poles, while the other five may occupy any position on the spindle. None are V-shaped as in a typical heterotypic anaphase. Counts of the chromosomes in the two daughter nuclei show in 7 cases $(7 + 0)$ distribution, in 25 cases $(6 + 1)$, 18 cases $(5 + 2)$, 15 cases $(4 + 3)$. The high frequency of the $(6 + 1)$ distribution indicates that the two members of the pair frequently separate, while the five univalents remain with one of them. In a single pollen mother cell this pair separated while the other five divided.

In the homotypic mitosis the chromosomes on the two spindles usually all divide, as observed also by Davis and Kulkarni, forming a tetrad. But frequently mother cells were observed containing a dyad of pollen grains, probably functional, or a hexad. The diploid *franciscana* has five pairs of chromosomes and a ring of four in diakinesis, and Emerson suggests that the associated pair in the haploid may represent two from this ring. As regards nuclear size, he finds that the mean diameters of the nuclei of the pollen mother cells in the diploid and haploid are respectively $12{\cdot}9\mu$ and $9{\cdot}6\mu$. This would give relative volumes of $1 : 0{\cdot}41$ or $2{\cdot}4 : 1$ (cf. Table II).

bud" from the egg should be regarded as an "attempt" at a division, seeing that something similar has been observed in haploid plants, is not certain.

In the sawflies, Peacock (1925) concluded from a study of *Pteronidea* (*Nematus*) *melanaspis* and other species that all male sawflies are haploid, but that occasionally a female is produced by parthenogenesis. In spermatogenesis of males there are two maturation divisions but no reduction of chromosomes ($n = 8$).

In the gall-flies both diploid and haploid parthenogenesis occurs, and Doncaster (1911) showed that in *Neuroterus* the males are haploid[1]. In the parasitic wasp, *Hadrobracon*, Whiting (1921) showed by genetic study of an orange-eyed mutation that while males are haploid they may in certain cases arise from eggs which have been fertilised. In general, there are two conditions as regards the equation division of the chromosomes in the haploid egg. It may be accomplished by an equal division of the cytoplasm, thus forming two functional sperms; or the second spermatocytes may be unequal, in which case only one functional spermatozoon is formed.

Among Homoptera, the greenhouse white fly, *Trialeurodes vaporariorum*, was found by Hargreaves (1915) to produce only females from the eggs of virgin females, while in America only males arose from such eggs. The English and American races thus differ in their parthenogenetic behaviour. This was confirmed by Williams (1917), who found very few males in England except in one collection from Hampshire. Schrader (1920) found that in the American race unfertilised eggs develop with the haploid chromosome number and produce males, while fertilised eggs are diploid and produce females. In spermatogenesis the haploid complex is retained, the reduction division is eliminated and only an equation division occurs.

Thomsen (1927) found both races of *Trialeurodes vaporariorum* in Denmark. No difference was discovered in the meiosis in the two types of eggs. Both undergo reduction ($n = 11$), but in the parthenogenetic eggs the diploid condition is restored, probably by splitting of the chromosomes.

Schrader (1923) has described in the mite (arachnid) *Tetranychus bimaculatus* (in which the females are conspicuously larger than the males) the same condition as in *Trialeurodes*. The haploid chromosome number is only three, all the eggs undergo meiosis, fertilised eggs form

[1] Doncaster found one mitotic figure with about $6n$ chromosomes in a developing muscle cell of a female.

embryos and larvae with six chromosomes, unfertilised with three. In the latter (males), though not many cytological details are given, it seems clear that the reduction division is omitted and a single equation division occurs.

There is some evidence of haploid parthenogenesis producing males also in rotifers (see A. F. Shull, 1929), lice and thrips, but these cases need not be entered into here. Both in phasmids and in the grouse locust, *Apotettix*, there is genetic evidence of segregation as well as crossing-over in the first generation of parthenogenetically produced offspring (Nabours, 1919, 1929); from which it may be concluded that chromosome reduction occurs in the unfertilised as well as in the fertilised eggs. Thus it appears that in Orthoptera generally all the eggs undergo reduction, parthenogenetic eggs with rare exceptions producing females, while fertilised eggs give a mixture of both sexes.

In Nematodes of the genus *Rhabditis*, although haploid males are not known to occur, yet the conditions resemble those already mentioned in certain plants. In *R. aberrans* (Krüger, 1913) males are extremely rare, the individuals being mostly hermaphrodite with the appearance of females. Sperms regularly enter the eggs, but degenerate there, while the egg develops parthenogenetically without chromosome reduction. Wilson (1925) calls this condition gynogenesis. In *R. pellio*, a related species, which is dioecious, producing males and females in nearly equal numbers, Paula Hertwig (1920) found in her cultures a mutant which produced diploid ($2n = 14$) females only. They and their descendants showed the same meiotic behaviour as *R. aberrans*, the eggs remaining diploid and developing parthenogenetically, but requiring the entrance of a sperm to stimulate their development. The sperm persisted in a compact form in the egg cytoplasm, even into the early cleavage stages. This interesting case shows that the condition of diploid parthenogenesis can arise directly from the normal sexual condition with haploid eggs and sperms. Similarly, as observed by Jørgensen in *Solanum nigrum*, the haploid egg was stimulated to develop by the presence of a degenerating male nucleus of *S. luteum*.

The case of the charophyte, *Chara canescens* (= *crinita*), shows certain points of similarity to *Rhabditis*. It has long been known that this species occurs in two forms, one haploid ($n = 12$) with male and female plants. This rare form is known only in certain scattered localities, *e.g.* Hungary and Sicily. When the oospore germinates, meiosis occurs, producing four nuclei, three of which degenerate. The other form is diploid throughout, is widely distributed and appears to be somatically

indistinguishable from the form with haploid gametophyte. It is always female and apogamous, the diploid egg developing without a reduction division when the oospore germinates. No doubt the latter condition was derived from the former, as in the parthenogenetic strain of *Rhabditis pellio*; but there is nothing to indicate what change in the fertilised egg of *Chara* led to the omission of meiosis when the oospore germinated. Ernst (1918) suggested crossing as the cause of the production of the parthenogenetic form, but this view is inadequate as an explanation, as Winkler (1920) has pointed out. Ernst assumed that if a simple doubling of the chromosomes had taken place in a haploid female, the resulting plant would be hermaphrodite; but from our present point of view we should expect it to be female, though probably stouter[1].

Winkler suggests two methods by which the diploid parthenogenetic female form may have arisen: (1) by chromosome doubling in an apical cell of the haploid female plant, (2) by union of two of the four haploid nuclei formed when the oospore germinates. He recognised from the Marchals' work on mosses that diploid gametophytes are not necessarily parthenogenetic, and he favours the origin of diploidy in *Chara* from an apical cell. Since two of the nuclei in the germinating oospore are presumably capable of producing a male gametophyte, and two a female, Winkler points out that fusion of two of these nuclei might give three different results: (*a*) ♂ + ♂ would produce a diploid male gametophyte which would die out, (*b*) ♀ + ♂ should produce a diploid hermaphrodite, (*c*) ♀ + ♀ would produce a diploid female, but there is no sufficient reason to suppose it would be parthenogenetic. None of these hypotheses explains at the same time the origin of diploidy and of parthenogenesis. On the other hand, we might assume that an unfertilised oogonium began to develop parthenogenetically and that doubling of the chromosomes occurred in the first cleavage of the unfertilised egg, but this gives no real explanation of the origin of the parthenogenetic behaviour. Winkler's hypothesis of origin from an apical cell of the haploid has at least as many difficulties. The widespread occurrence of the diploid indicates that parthenogenesis is a success.

In *Icerya purchasi* (Coccidae) Schrader and Hughes-Schrader (1926) have clearly shown that hermaphrodites have four chromosomes in the somatic and oogonial tissue, while males have two chromosomes in all their somatic and spermatogonial cells, *i.e.* they are haploid throughout, their nuclei and cells being decidedly smaller in the early stages of

[1] Though not necessarily. Cf. haploid and diploid generations in *Polysiphonia* (Yamanouchi, 1906).

development, but with many adjustments of size later. A single meiotic division is conclusively shown in the males, since each cyst contains 16 nuclei before meiosis and 32 nuclei, producing 32 sperms, afterwards. The germ cells of hermaphrodite embryos are shown by Hughes-Schrader (1927) to be diploid (four chromosomes). But at the time of the first nymphal instar, haploid nuclei appear among the diploid. How they arise is not known, but from this haploid tissue arise the sperms of the hermaphrodite gonad. In spermatogenesis, both in hermaphrodites and in haploid males, there is but one meiotic division (equational). In two aberrant cases, however, the spermatids as well as eggs arose from diploid cells. There were then two reduction divisions, but without synapsis. The same racial conditions, with diploid hermaphrodites and haploid males but no females, were found both in Italy and America.

In the Coccidae, *Lecanium hesperidium* and *L. hemisphæricum*, Thomsen (1927) has found that both species occur in two races, (1) a purely parthenogenetic race of females only, (2) a bisexual parthenogenetic race of males and females, the latter in the minority. In the former race the eggs undergo one equation division with $2n$ chromosomes, but with neither synapsis nor the formation of chromatin tetrads. The eggs of the bisexual race undergo the reduction divisions, but in unfertilised eggs the $2n$ number of chromosomes is restored by fusion between the egg nucleus and the second polar body. The females so produced are thus diploid, and the nuclear fusion is said to be extraordinarily like fertilisation.

Parthenogenetic development has been experimentally produced, especially in sea-urchins, starfish, annelid worms, molluscs and frogs, but only frogs have been reared to maturity by these methods, although starfish and sea-urchins have developed through metamorphosis. It is clear that the embryos are haploid in the beginning of their development, at least in those cases, such as the sea-urchin, where the polar bodies are formed before the egg is stimulated to develop. Shearer and Lloyd (1913) counted the haploid chromosome number (18) in *Toxopneustes* and *Strongylocentrotus* larvae which had undergone metamorphosis, so it is probable that such individuals would remain haploid as adults. The parthenogenetic haploid larvae were readily distinguishable from normal diploid plutei. Their arms were one-third longer, the protoplasm slightly granular, less transparent, and the pigmentation more scattered. They also developed much faster up to the 4- and 8-armed pluteus stage, and after that much more slowly, metamorphosis taking place in 8–10 weeks instead of 5–6 weeks. Metamorphosis pro-

ceeded so slowly that the larvae starved before it was completed, which apparently accounted for their death at this time. They appear to have remained haploid throughout, but were not visibly smaller than diploid plutei, and the nuclear sizes were not compared. Delage had previously succeeded in rearing six parthenogenetic sea-urchin larvae through metamorphosis, two of them attaining sufficient sexual maturity to be identified as males.

Similarly in the annelid *Thalassema* and the mollusc *Cumingia*, cleavage of the egg has been observed to take place with the haploid chromosome number. It is equally clear, however, that in many cases the diploid number is restored after development of the egg begins. The various ways in which this may happen need not be discussed here.

The parthenogenetic frogs of Loeb (1918), obtained by pricking the egg with a needle, proved to be 15 males, 3 females and 2 doubtful. Some males reached full adult size at an age of 10–18 months and were entirely normal. There is very little doubt that all those, both males and females, which reached maturity were diploid. In another lot of 65 frog larvae parthenogenetically produced by Loeb, Parmenter (1920) counted the chromosomes of 14 individuals, including one male frog and 13 tadpoles. In every case the number was diploid (26) or nearly so. It is not known where the doubling takes place, but since mortality is high in the early stages of development, it is reasonable to suppose that only those larvae survive in which doubling of the chromosomes took place sufficiently early, larvae with some haploid and some diploid tissue having a high death rate. Hovasse (1922) has since counted chromosome numbers from 8 to 27 in parthenogenetic frog larvae, but mostly approaching the haploid or diploid numbers. Among the young embryos and larvae studied, 75 had about 24 chromosomes (which he regarded as the diploid number), 65 had about 12 chromosomes and 14 had other numbers. The haploid numbers were more frequent in the early stages, up to 24 hours, while the oldest larvae (18 to 84 days) were all diploid. The conclusion seems clear, although Hovasse denies that differential mortality is at work here. The cleavage spindles in presumably haploid frog eggs are much smaller than normal. Also the rate of development is less in parthenogenetic than in normally fertilised eggs.

Among various studies of the effects of radium emanation on the eggs and sperm of frogs and toads, G. Hertwig (1913) found that when eggs were inseminated with strongly irradiated sperm of another species, the foreign chromatin was soon eliminated from the eggs, which were stimulated to develop gynogenetically. The tadpoles so produced were

conspicuously smaller than normal ones of the same age, and usually showed various imperfections although they developed at about the normal rate. Their nuclei were evidently haploid since they had practically half the volume of the nuclei in corresponding tissues of normal larvae, *e.g.* in the medulla and the liver. It appears highly probable that in those tadpoles, unlike the parthenogenetic frogs of Loeb, the haploid chromosome number was retained. In such experiments, however, in some of which the egg rather than the sperm was irradiated, leading to inactivation of the egg chromosomes (see also Wilson (1925), p. 463), some tadpoles were of normal size and with larger, evidently diploid, nuclei. These also probably began their development with a single set of chromosomes (maternal or paternal) as in Loeb's parthenogenetic frogs.

The number of methods hitherto used to obtain haploid parthenogenesis is greater in animals than in plants. They include hypertonic sea-water, addition to the medium of neutral salts (such as KCl), CO_2 and weak acids or bases, and also physical agencies such as increased osmotic pressure, mechanical shaking or puncture, temperature changes, radium, or electrical stimulus. The work of Baltzer, Doncaster and Gray, and Tennant showed that in cross-fertilisation of echinoderm eggs with sperm of another species or genus the paternal or maternal chromosomes, or some of each, might form vesicles and be eliminated from the egg, which then gave rise to larvae with corresponding characters and in some cases haploid nuclei. In various experiments which need not be detailed here, when eggs were cross-fertilised after having begun parthenogenetic development, the resulting larvae were in some cases mosaics of cells with different nuclear content, some of them containing only the paternal chromosomes. In inter-generic echinoderm crosses of Baltzer the paternal chromosomes may be retained in the nucleus until blastula formation, when elimination of the paternal chromatin takes place. Irradiated sperm, in the experiments of G. Hertwig cited above, stimulated the eggs to parthenogenetic development without themselves taking part in nuclear formation, but apparently no case is known in animals where, as in plants, the normal sperm of another species has entered the egg and disintegrated, thus causing its parthenogenetic development.

The described cases of segmenting ova in virgin mice and rabbits are presumably to be classed as "spontaneous." In this connection, Baltzer's (1922) success (following Spemann) in rearing a *Triton* larva through metamorphosis from an enucleate egg fragment fertilised by a

sperm is noteworthy. The larva was doubtless haploid, since its nuclei were only half the normal size. Boveri had shown earlier that enucleate fragments of sea-urchin eggs, if entered by a sperm, could develop merogonically into dwarf (haploid) larvae.

It thus appears that while, in plants, haploid adults can be reared to maturity, in animals they usually either double their chromosomes during development, or fail to reach maturity. If haploid animals actually attained maturity, they might be expected to be more or less completely sterile, as are haploid plants, but no such case appears to have been recorded resulting from artificial parthenogenesis, although Baltzer's case of merogony in *Triton* is closely similar. On the other hand, natural haploidy such as occurs in the males of various animals is unknown in seed plants.

Light is thrown on several problems of haploidy in animals by the occurrence of two haploid-diploid mosaics in *Drosophila*, described by Bridges (1925). In a genetic cross which produced "piebald" individuals, there were spots of tissue in which the recessive paternal characters were shown and the maternal X-chromosome had apparently been lost, the rest of the individual being female and presumably normal diploid, showing the dominant maternal characters. One individual differed from the rest in having the whole left side of the head different from the right in several genetic characters and also notably smaller. Without going into details, the genetic evidence seems clear that the left side of the head was strictly haploid and paternal, all the maternal chromosomes (containing dominant characters) having been eliminated. Bridges points out that, on the theory of genic balance, an individual with $1n$ chromosomes should be female, and this was borne out in so far as the left eye took the tinge which the eosin mutation shows in the female as distinct from the male. An unsuccessful attempt was made to measure the cells and nuclei on the two sides of the head, but the eye facets in the left eye were shown to be conspicuously smaller than those of the right in the ratio 19 : 23. In a triploid fly they were correspondingly larger, and ommatidium size is probably an accurate index of cell size.

In another cross there appeared, besides piebalds, another individual which was apparently a haploid-diploid mosaic on a larger scale; the left wing was only three-fourths the normal size, the three left legs were shorter and more slender than the right ones, and the left fore-leg bore no sex comb, the absence of a sex comb being strong evidence that the tissue was female in nature as well as presumably haploid.

Although haploids are non-viable in *Drosophila*, these haploid-

diploid mosaics appear to confirm the view that haploids with one set of autosomes and one X would be females, just as diploids with two sets of autosomes and two X-chromosomes or triploids with three such sets and three X's are females. This leads to a somewhat contradictory position, since as we have already seen in cases of normal haploidy in animal species the haploid individuals appear always to be males in the various groups of animals in which they occur.

In seed plants, on the contrary, the haploids are, as might be expected, hermaphrodite like the diploids from which they are derived. Incidentally the production of haploid sporophytes differing from the diploid mainly only in size would be a fatal blow to the theory of antithetic alternation of generations in plants in its old form, had not that theory already been largely given up; for it renders untenable the view of the sporophyte as a post-sexual phase intercalated between two gametophyte generations, and differing in morphology because of its double series of chromosomes. The fact that marked and sudden changes can take place in the life cycles of various plants and animals will lead to a much wider introduction of mutation conceptions into the explanation of such differences in life cycles as we have been discussing. Some of these questions, in so far as they relate to the Thallophyta and the Protista, have recently been discussed by Hartmann (1929).

It seems clear that the condition of haploid males and diploid females has been derived independently in different animal groups from ancestors with the normal bisexual conditions; and presumably some changes in the chromosome relations have occurred, which at the same time render haploids viable and lead to a redistribution of factors for maleness and femaleness which results in haploids being male. Schrader and Sturtevant (1923) discussed the difficulty mentioned above, namely that in some animal groups the haploids are normally males, whereas in *Drosophila* and presumably in all bisexual animals in which the female sex is homogametic, the tissue of the haploid and therefore the haploid itself may be expected to be female, since the effective relation is the ratio between the X-chromosomes and the autosomes. The subsequent discovery of haploid-diploid mosaics in *Drosophila* by Bridges lent strength to this view. They suggest that maleness and femaleness have different threshold values in a continuous series, the resulting sex as diploid male, haploid male, intersex or female depending on the relative number of sets of sex chromosomes and autosomes. Some quantitative view of the male and female sex factors, such as that of Goldschmidt, as well as of the rest of the germplasm in relation to sex, is necessary to account for these

various relations; but before they can be understood, further cytological investigations of the life cycles in various animals showing haploid parthenogenesis will be necessary, both as regards the history of the autosomes and of the sex chromosomes. While this is not the place to discuss sex determination, yet it is recognised now that both autosomes and sex chromosomes carry factors which quantitatively influence the sex of the individual during periods of its ontogeny.

SUMMARY.

1. A new case of haploidy in *Oenothera* is described. It arose from *Oe. rubricalyx* pollinated by *Oe. eriensis*. The hybrids produced are non-viable, dying in a few days. Two seedlings in a family of 85 persisted and one, which survived to maturity, was haploid. It was conspicuously smaller, with various morphological changes, and was completely sterile in pollen and seeds.

2. This haploid has smaller cells, and series of measurements (see Tables I–III) show that the ratio of decrease corresponds in general with that of increase in size in various tissues of the tetraploid. Neither the haploid nor the tetraploid corresponds cell for cell with the diploid. Both the haploid and the diploid usually have four wall layers in the anther, but whereas the haploid sometimes has five layers of small cells the diploid may have only three layers of larger cells.

3. The various cases of haploid sporophytes in flowering plants and of animal species in which the males are haploid are reviewed, also the chromosome relations in artificial parthenogenesis. Although haploid plants can be reared to maturity, haploid animals usually either fail to reach maturity or double their chromosomes during development.

4. Haploid sporophytes have been described in eight genera of flowering plants—*Datura*, *Nicotiana*, *Triticum*, *Solanum*, *Brassica*, *Matthiola*, *Crepis* and *Oenothera*. The haploids are smaller than the diploids, with smaller cells, showing also certain alterations in form and sometimes in flower colour, and they are almost completely sterile. Such meiotic peculiarities as a unipolar heterotypic spindle and functional pollen dyads may occur. Haploid plants have appeared, (*a*) after crossing, especially with a distantly related species, (*b*) after subjection to cold at the time of fertilisation, and (*c*) in the tomato, "spontaneously."

5. The existence of haploid sporophytes is contrary to the theory of antithetic alternation of generations in plants, at least in its older form.

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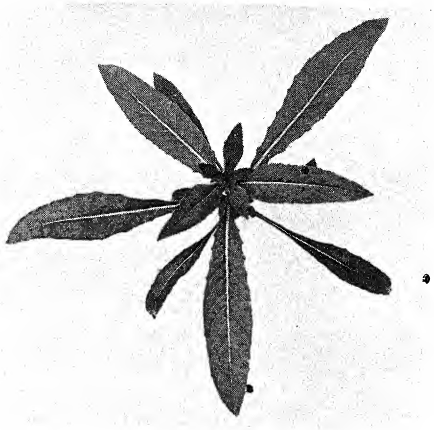
EXPLANATION OF PLATE VII.

Fig. 1. *Oe. eriensis* × *rubricalyx*, F_1, rosette.
Fig. 2. *Oe. eriensis* × *rubricalyx*, in flower.
Fig. 3. Haploid *Oe. rubricalyx*, from *rubricalyx* pollinated by *eriensis*.
Fig. 4. Haploid *Oe. rubricalyx*, in flower.
Fig. 5. Somatic metaphase showing seven chromosomes in haploid.



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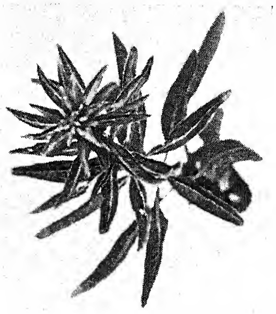

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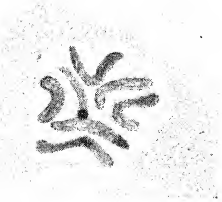

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THE SEX RATIO IN *ASPARAGUS OFFICINALIS* L. AND ITS ARTIFICIAL MODIFICATION.

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(With Five Text-figures.)

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PART I. THE NORMAL SEX RATIO.

INTRODUCTION.

IN recent years numerous publications have appeared concerning sex in asparagus, a normally dioecious plant. These have attracted the attention, not only of the botanists and horticulturists, but also of commercial concerns dealing with this crop, since sex seems to have a profound effect on the yield of the marketable asparagus. The writer was engaged in work on the sex segregation of asparagus with the California Packing Corporation from the beginning of June until the end of December 1926.

During the course of this work some facts were observed which were not in agreement with previous statements, and it is hoped that the fresh data here presented may be of some benefit from the scientific aspect as well as from the commercial point of view.

HISTORICAL REVIEW.

Tiedjens (1924), in studying the physiological aspects of asparagus, noted that staminate plants produced 25 per cent. higher yield and held

up better from year to year; although pistillate plants produced a greater percentage of *A* (large) spears. He also showed that in a large number of plants there was a decided uniformity in the number of buds produced from year to year, suggesting a genetical factor.

The superiority of staminate plants as shown by Tiedjens seems reasonable; for in the production of asparagus spears, buds are formed previous to the period in which they develop into spears. It is probable that in the production of seeds on the pistillate flowers some of the food reserves are utilised, which may inhibit bud formation as compared with staminate plants. The remarkable work of Kraus and Kraybill (1918) on tomato plants has shown that nutritional disturbances (carbohydrate-nitrogen relationship) affect the fruit production quite materially. Kraus and Kraybill's findings, in the main, have been supported by other workers such as Roberts (1920), Kraybill (1923), Hooker (1925), Murneek (1927), Paddock and Charles (1928), and Bailey (1928). Green (1890) compared 50 staminate asparagus plants with an equal number of pistillate plants for a season. He found a gain of nearly 50 per cent. in favour of staminate plants. He further noted that the yield was proportionately greater in the early part of the cutting than in the later.

The writer's experience, in observing asparagus fields for three years, confirms this last statement of Green. In all varieties, staminate plants begin to send off spears earlier in the season than pistillate plants of the same variety, under the same conditions. The writer observed in the early part of January (at Montezuma Ranch, California Packing Corporation, in 1–6 year old plantings of Mary Washington) 3–4 in. tall asparagus spears from the buds of staminate plants. The same height of spears in female plants was not attained until a month later.

Thompson (1923) showed that in the Mary Washington strain of asparagus male plants produced more spears, but that the proportion of "giant" asparagus was smaller than in female plants. These results have been questioned by Green.

Böttner (1921) also noted the superiority of male as compared with female plants. He also observed that in young asparagus plantings there were equal numbers of male and female plants, but that in older plantings there was a preponderance of staminate individuals.

During the last few years, considerable data have appeared from studies made at the California University Farm, Davis, California. In 1925 Robbins and Jones showed that, in both Mary Washington and Palmetto, staminate plants produced more spears, and greater weight of spears, during the first cutting season than did the pistillate.

This difference was proportionately greater during the early part of the cutting season than during the later part. Their data showed the same results during the second season of growth. They also adduced field observations showing that in commercial asparagus fields there were virtually equal numbers of staminate and pistillate individuals.

It must be pointed out that in Robbins and Jones' discussion, Table I (Ratio of Staminate and Pistillate Plants in the Field) does not indicate the variety or varieties of asparagus (Palmetto, Mary Washington or both) from which their data were obtained. Actually these two varieties show some variation in the sex ratio in the field. Further, their data were collected from May to September 1923, and only once on each of the ranches mentioned, while field observations show that asparagus plants continue to express their sex in November, and even in December. They appear to have examined only 97 plants at California Packing Corporation, Ryer Island, and 137 plants at Montezuma Ranch, Collensville—a very small proportion from a planting of about 17,000 acres. Below we shall present data derived from some of the ranches in which Robbins and Jones obtained their figures which show that a single counting is not reliable.

Robbins and Jones (1926) subsequently confirmed the results of their earlier paper and brought forward more data to show the superiority of male plants as compared with female plants in commercial plantings. Still more recently they (1928) have published the results of further studies on sex in asparagus, stating that the staminate plants produce a larger number and greater weight of stalks than the pistillate plants, as well as more spears per plant and a higher yield per acre, but that the average size of the spears is somewhat smaller.

The work of these different authors offers sufficient experimental evidence of the superiority of staminate plants over the pistillate for higher yield of spears. Certain workers have also shown that there are generally equal numbers of male and female asparagus plants in commercial plantings, and it is to this last statement that the data in this paper refer.

Material and methods.

Land on Montezuma Ranch (California Packing Corporation) was selected for asparagus nursery plantings. Table I[1] shows the date of seed planting, the field number, acres, variety and the weight of the asparagus seeds.

The beds were prepared according to the directions of Jones and

[1] For these data I am indebted to Mr R. O. Cook of the California Packing Corporation.

Robbins (1924). The seeds were sorted, and only mature and unblemished seeds were used. Before planting they were soaked for 4½ days at 86° F. as recommended by Borthwick (1924). The soil for field number 65 was analysed physically and chemically, and it was found that all plots were

TABLE I.

Asparagus nursery plantings, 1926.

Date planted	Field no.	Acres	Variety	Seed planted (lb.)
23. iii. 26	40	24·17	Mary Washington	472
26. iii. 26	47	10·00	,,	258
27. iii. 26	65	6·67	,,	37½
27. iii. 26	65	6·67	M.W. Tract 2, 1925	6
27. iii. 26	65	6·67	M.W. Regular	31
27. iii. 26	65	6·67	M.W. Tract 2, 1924	48
27. iii. 26	65	13·93	Ryer Palmetto	340
5. v. 26	48	8·0	Mary Washington 2	154

approximately alike in these respects. Mary Washington seeds were used, since their superiority has been shown by Norton (1924), Robbins (1926), Anonymous (1924), and Wheeler (1922). Palmetto was also grown, since it shows some resistance to rust as noted by an anonymous writer (1925), and by De Fabery (1916). In general all standard cultural methods, such as hoeing, cultivation, irrigation, were followed as commonly practised in the Delta region.

In the latter part of June blossoms began to appear. Two adjacent nursery plots showed very uniform growth. From this time until the end of December the sex was determined, counted and recorded. Each plant as determined for sex was tagged. Blue tags were used for staminate flowers and red tags for pistillate. The field was run over daily, and a record of the blossoms appearing was taken. At the end of the season the data were collected together and arranged according to Fisher (1925).

Simultaneously a second study was carried out on plants grown in 1–5 year old beds on the same ranch. No tags were used in this case. The data were arranged in the same way as above, and the results will be discussed elsewhere in this paper.

Several 2–4 year old male and female asparagus (Mary Washington) crowns were secured in November 1927 from Sutter Basin Company. They were grown in the open in pots on Berkeley Campus of the University of California, and observations on their growth were made until the end of July 1928 (cf. Figs. 1 and 2).

For the general identification of male and female flowers, drawings

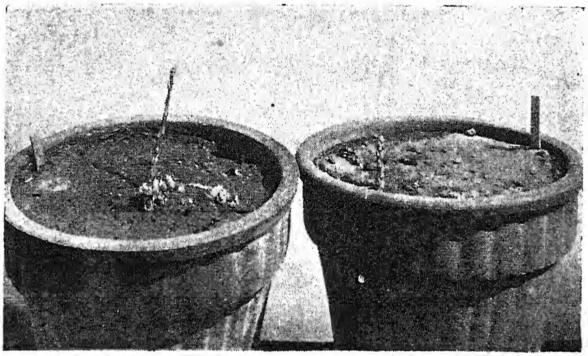

Fig. 1. Mary Washington asparagus male plant (right), female plant (left). Note the growth made by these plants in 4 weeks, after growing the crowns in the pots.

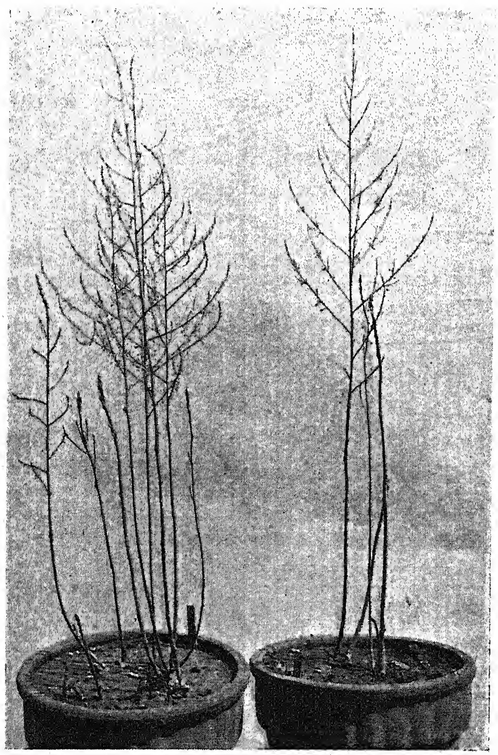

Fig. 2. The same plants as in Fig. 1 about 2½ months later, male on left, female on right. Note the greater number of shoots and greater amount of growth in the male plant as compared with the female. This was typical of 50 pots. All crowns used were of the same weight and all environmental conditions were identical.

of these flowers at two stages were prepared. They show the typical morphological differences between the two kinds of flowers (cf. Figs. 3 and 4).

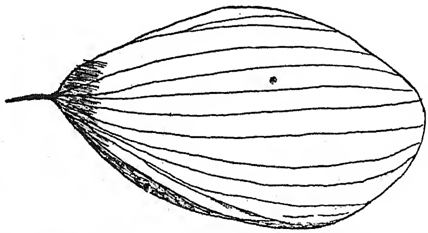

Fig. 3 *a*. A typical staminate flower of Mary Washington strain of asparagus in an early stage.

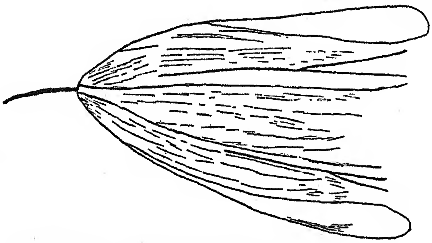

Fig. 3 *b*. The same kind of flower when open.

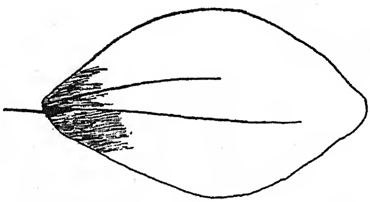

Fig. 4 *a*.

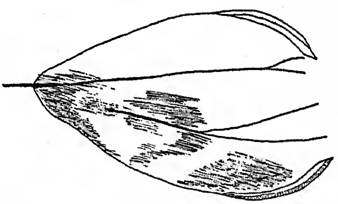

Fig. 4 *b*.

Fig. 4 *a*. A typical pistillate flower of asparagus (Mary Washington) in the same stage as the staminate flower in Fig. 3 *a*. Note the difference in appearance as to size and shape, especially toward the tips of the flowers. All flowers are much enlarged.

Fig. 4 *b*. A typical pistillate flower from the same plant (as above) and in the same stage of development as flower in Fig. 3 *b*. Note the difference at the tips in both kinds of flowers.

Results.

It will be seen from Table II that both Palmetto and Mary Washington plants grown from seed showed differences in the sex ratio during their first year, under Californian conditions. In both varieties the percentage of staminate plants was smaller than the percentage of pistillate plants. The figures were based on the counts which were carried out continuously from August to December.

TABLE II.

Relation of staminate and pistillate plants during the first year after planting of seeds.

Field no.	Variety	No. of plants counted	Staminate (%)	Pistillate (%)	Plants not in bloom (%)
65	Mary Washington	34,240	28·9	60·1	11·0
65	Palmetto	7,629	33·1	58·5	8·4

The data also show that in Mary Washington there was lower percentage of staminate plants than in Palmetto, while the percentage of pistillate flowers was the reverse. Further, the last column shows that in the first year 11·0 per cent. of Mary Washington did not flower, while for Palmetto the percentage was 8·4. There were very heavy frosts on December 15th and 16th, which might have checked further blossoming; and a heavy wind from December 1st to 8th, which might have caused many berries and blossoms to fall.

This ratio of staminate and pistillate plants differs from that shown by Robbins and Jones; but since their counts were of 1 or 2 year old beds, these data are by no means comparable with their Table I.

In order to obtain comparable data observations in some of the fields in which Robbins and Jones counted asparagus plants were made throughout the season. At the end of the season these records were compiled, and will be discussed below.

Sex ratio in 1–5 *year plantings*. The ratio of staminate and pistillate plants in 1–5 year old commercial plantings is shown in Table III. The data in columns IX and X seem to indicate that in both the ranches a lower percentage of staminate plants was found than pistillate, and this occurred in both varieties of asparagus observed. The data also indicate, for beds set in the same year, a lower percentage of staminate flowers in Mary Washington than in Palmetto. This percentage was reversed in the case of pistillate plants. Two points are worthy of note. First, that the bed set in 1921 had a slightly lower percentage of staminate plants than beds set in 1925 (Ryer Island Ranch) and in 1923 (Montezuma Ranch). The percentage of pistillate individuals was higher in the older than in the younger beds. Two explanations seem plausible. In the younger beds, the percentage of plants not in flower was higher than in the older beds. If most of these were potential pistillate plants, the percentage of staminate plants would have been decreased. Secondly, as the asparagus beds became older some asparagus plants must have died, and mortality may have been higher for male than for female. To test

TABLE III.

Ratio of staminate and pistillate plants in 1–5 *year old commercial plantings.*

(Observations made between June and November 1926.)

I	II	III	IV	V	VI	VII	VIII	IX	X	XI
			Robbins and Jones' data				The writer's count			
Ranch	Location	Bed set	No. of plants observed	Staminate (%)	Pistillate (%)	Plants not in bloom (%)	No. of plants observed	Staminate (%)	Pistillate (%)	Plants not in bloom (%)
California Packing Corporation	Ryer Island	1921	97	50·5	48·4	1·1	T. 1856	—	—	—
							M. 950	30·1	69·9	0
							P. 906	35·7	64·2	0·1
		1922	—	—	—	—	T. 1121	—	—	—
							M. 602	29·9	69·3	0·8
							P. 519	36·2	63·68	0·12
		1923	—	—	—	—	T. 1102	—	—	—
							M. 590	30·4	68·5	1·1
							P. 512	37·0	61·9	1·1
		1924	—	—	—	—	T. 809	—	—	—
							M. 459	30·0	68·69	1·31
							P. 350	37·7	61·0	1·3
		1925	—	—	—	—	T. 790	—	—	—
							M. 401	33·0	65·2	1·8
							P. 389	37·2	61·1	1·7
Montezuma Ranch	Collensville	1921	137	51·8	48·2	0	T. 967	—	—	—
							M. 522	31·5	68·5	0
							P. 445	38·1	61·1	0·8
		1922	—	—	—	—	T. 823	—	—	—
							M. 511	33·1	65·8	1·1
							P. 312	38·7	59·7	1·6
		1923 ?		—	—	—	T. 722	—	—	—
							M. 401	30·7	67·9	1·4
							P. 321	45·1	53·1	1·8

Note. T. = Total plants observed (Mary Washington plus Palmetto).
M. = Mary Washington plants observed.
P. = Palmetto plants observed.

this possibility the writer walked through the asparagus rows in both of these ranches (1926), and found that of 87 unrecoverable plants 51 (approximately 59 per cent.) were staminate. A comparison of these figures with those taken from Table I of Robbins and Jones shows (even for the bed set in the same year) that the results do not coincide. In one case, however (1923), my figures approximate to those shown by these authors, viz. for Palmetto plants in Montezuma Ranch (bed set in 1923). Since in all other cases the percentage of staminate asparagus plants (both Mary Washington and Palmetto) is lower than that of pistillate plants, it is difficult to accept Robbins and Jones' results.

Summary.

1. Sex ratios were determined in two commercial varieties of asparagus (Mary Washington and Palmetto) grown under Californian conditions.

2. Working with asparagus plants grown from seed, as well as plants grown in 1–5 year old beds, it was found that there was a lower percentage of staminate plants than pistillate. There was only one case where the ratio noted was about equal.

3. The data show about 29 ± 3 per cent. staminate plants and 65 ± 5 per cent. pistillate plants.

4. Mary Washington usually had fewer staminate plants than Palmetto.

5. Observations of the commercial asparagus plantings, as well as qualitative determinations in plants grown from 4 year asparagus crowns, showed that staminate plants yielded more than pistillate plants.

6. It is a prevailing opinion among farmers as well as among scientists that Mary Washington is a more desirable strain of asparagus. Since some workers have shown quantitatively, and this study has shown qualitatively, that staminate plants yield more than pistillate, it is very essential to have a higher percentage of staminate plants grown in the field.

PART II. ARTIFICIAL MODIFICATION OF THE SEX RATIO.

MATERIAL AND METHODS.

It is known that under normal conditions of pollination many dioecious plants exhibit a varying excess of female plants; though in certain cases Correns obtained a marked increase in the proportion of males. These results indicate that there may be two classes of pollen grains, namely, female determining and male determining, and that under competitive conditions the former are favoured. The writer has always wondered whether the basis for differentiation into these two classes was physiological or genetic. This is of particular significance when we consider the importance of size, shape and colour reaction of pollen carbohydrate grains, as pointed out by Sears and Metcalf (1926–7). Whether these chemical reactions be considered of any importance in the genetic analysis or not, it is worth while to consider the carbohydrate changes in pollen before any experiments on pollination be conducted. Such factors as temperature ought to be considered. This seems necessary, because these (physiological) considerations might influence the chromosome equipment. Furthermore there may also be numerous cases in which digestion rates of pollens may supply criteria with reference to genetic factors.

In July 1926, matured pollen was collected from Mary Washington

asparagus plants, produced from 4 year old crowns. The trophic and environmental conditions of the bed into which these crowns were transplanted were very uniform. About 800 plants (free from any visible effects) were selected at Montezuma Ranch California Packing Corporation. Only matured pollen was used throughout the course of this study. The importance of matured pollen has been emphasised by many workers, including Bond (1927), whose paper appeared during the course of this study.

Pollen was collected in small air-tight phials and tested for maturity under the microscope. It was divided into four equal lots, *A*, *B*, *C* and *D*. All of these processes were carried out on the same day. From field observations it was noted that fresh pollen gave a peculiar odour, which decreased as it aged.

The writer assumed that the chemical cause of this odour was some essential oil or oils, which contained a fair percentage of ester. This chemical or chemicals seemed to be volatile; hence the diminution of odour might have been due to the passing off of these oils. It is conceivable that the presence, absence or abundance of these chemical substances might have some effect on the activity of pollen. If this be true, it is also conceivable that a decrease or increase of these substances might affect the functioning of pollen qualitatively as well as quantitatively.

To test the above assumption pollen of lot *A* was further divided into three portions, *a*, *b*, *c*. Portion *a* was exposed for 6 hours, *b* for 12 hours and *c* for 24 hours. Pollen of lot *B* was put in a distilling flask. Volatile oil or oils were distilled, with a very gentle current of steam by means of steam distillation, following the directions of Houben (1921). Preference was given to this method because it has been shown by Perry (1911) that the extraction of essential oils by steam distillation is the most common and generally applicable method. About 13 c.c. of distillate were obtained. This was further distilled by a Wurtz flask to separate the distillate into fractions at the negative pressure of 10 mm. with the equipment recommended by Allen. Three fractions were obtained, of which only the first was used because it was found that the substances with low boiling points gave more odour than the others. Walker (1913) has shown that a higher percentage of volatile oil is distilled in the first fraction than in the fractions following; assuming that the boiling point of the oil is lower than that of the associated liquids. Thus it was necessary to use only the first fraction, whose volume was 5·3 c.c.

The apparatus for gentle spraying of the distillate was prepared as shown in Fig. 5. This was constructed on the principle of a simple nose and throat atomiser. The hole for spraying was much smaller (to ensure a fine spray) and a small graduated tube for holding the liquid was sealed to the base. Pollen of lot C was divided into three portions. Three slides, commonly used for hanging drop studies, were thoroughly cleaned, dried in an oven at 65° C., allowed to cool in a desiccator (containing sulphuric acid), and weighed (up to four decimal places) until a constant weight was maintained. These slides were labelled 1, 2 and 3. The three portions of pollen from lot C were poured into each of the slides and weighed. The difference between the weights of the slides, plus pollen, and the empty slides gave the net weight of the pollen in each slide.

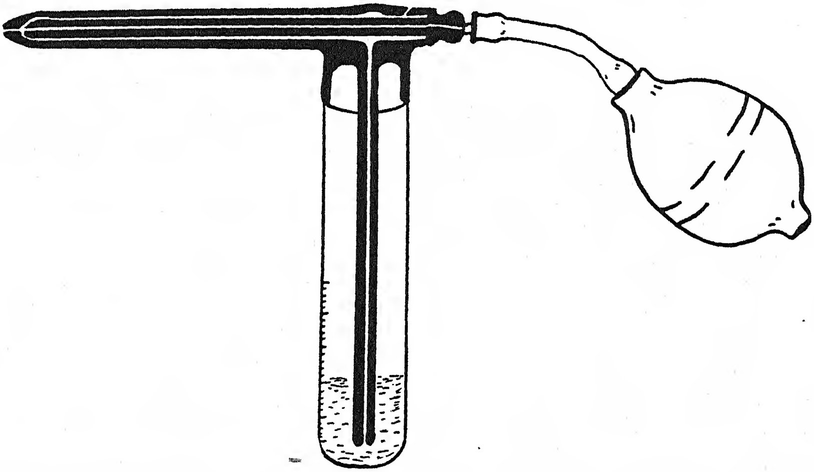

Fig. 5. An apparatus for spraying pollen with distillate (obtained from the pollen) or water. *Note.* Graduated tube to hold the liquid enlarged twice.

The distillate (presumably volatile oil) was sprayed by means of the apparatus mentioned above. Each time a small quantity of liquid was sprayed very evenly and gently on pollen. The increase in weight was followed very carefully. Spraying was stopped when pollen in portion 1 increased 10 per cent. of its weight; in portion 2 increased 30 per cent.; and in portion 3 increased 60 per cent. The slides were immediately covered with clean cover glasses and sealed with wax. This was necessary to prevent the escape of the sprayed liquid. The cover glasses were taken off immediately before pollination.

Pollen of lot D was divided into three portions and put in three hanging drop slides. They were sprayed with distilled water by means

of the apparatus used previously for lot *C*. The slides were also treated in the same way as those recorded before. Spraying of distilled water was stopped, when portions 1, 2 and 3 increased 10, 30 and 60 per cent. of their weight respectively. These portions of lot *D* served as checks. This was essential, since it was assumed that a unit volume of water could not bring about the change in activity of pollen which a unit volume of volatile oil could. The slides after spraying were sealed in much the same way as the slides of lot *C*. About 100 normal pistillate Mary Washington asparagus plants of the same bed were selected. While the flowers were still unopened, they were covered with small paper bags. When the flowers opened, the pollen of each of the three portions of lots *A*, *B* and *C* was applied by means of a camel's-hair brush. The flowers were again covered by the bags for 4 days. About six to eight flowers on each plant were pollinated. The berries produced were picked at maturity on November 25th and the seeds removed. About 120 to 125 seeds were secured from each of the three portions of lots *A*, *C* and *D*.

On February 25th, 1927, these seeds were planted in nine rows. Before planting, they were soaked for 4½ days in water maintained at 65° F. This was necessary for better and quicker germination as discovered by Borthwick (1924). Observations to determine the sexes of the flowers were made from July to November 1927. In July about 30 more plants were treated in a manner similar to lot *C* of 1926, namely, with volatile oil. These portions yielded 102, 110 and 118 (total 330) seeds respectively. They were planted in January 1928 in the Horticulture Greenhouse, University of California, Berkeley, and allowed to grow until the end of July 1928. In both years staminate, pistillate and non-blossoming plants were counted and tabulated.

Results.

Table IV shows the absolute numbers and percentages of staminate and pistillate plants from pollen which was treated in the several different ways. Columns VI and VII show the number of staminate and pistillate plants. The data indicate that, as the exposure period was increased (lot *A*, portions 1 to 3) from 6 to 24 hours, the absolute number as well as the percentage of staminate plants decreased. It is assumed that by such an exposure of the pollen, some water and volatile oil may decrease. As these two components of the pollen grains diminished, the percentage of staminate plants decreased, while that of pistillate increased. Column VIII seems to show that by this treatment of the pollen the number of non-blossoming plants increased. It is seen from the data that pollen

TABLE IV.

Data showing the ratio of staminate and pistillate asparagus (Mary Washington) plants, as modified by the pollen, which was treated as mentioned.

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
				Plants secured				Percentage		Percentage excluding non-blossoming plants	
Year	Lot and portion no.	How treated	Seeds planted	Total	Staminate	Pistillate	Non-blossoming	Staminate	Pistillate	Staminate	Pistillate
1927	*A* 1	Exposed 6 hr.	120	117	38	69	10	32·4	58·9	35·5	64·5
	2	,, 12 ,,	120	119	36	72	11	30·2	66·0	33·3	66·7
	3	,, 24 ,,	120	115	31	71	13	27·0	61·7	30·4	59·6
	C 1	Sprayed with volatile oil until 10 % increase in wt.	124	121	52	60	9	43·0	49·5	46·4	53·6
	2	Increase 30 %	124	123	69	45	9	56·1	36·6	60·7	39·3
	3	,, 60 %	124	110	69	30	11	58·5	32·2	64·5	35·5
	D 1	Sprayed with water until 10% increase in wt.	120	114	40	63	11	35·1	55·3	38·8	61·2
	2	Increase 30 %	120	117	42	66	9	35·1	56·5	39·8	60·2
	3	,, 60 %	120	118	41	66	11	34·7	55·9	38·3	61·7
1928	*C* 1	Sprayed with volatile oil until 10 % increase in wt.	102	101	45	53	3	44·5	52·5	45·9	54·1
	2	Increase 30 %	110	107	57	42	8	53·2	39·2	57·5	42·5
	3	,, 60 %	118	111	59	42	10	54·0	37·8	58·4	41·6

in various portions of lot *C* showed just the reverse of lot *A*, namely, that when pollen (portion 1) was sprayed with volatile oil (distillate) until the pollen gained 10 per cent. of its weight, the number as well as the percentage of pistillate plants decreased while staminate plants increased. The same happened for portions 2 and 3, although there was not much difference between them. It was also noted that the number of non-blossoming plants was less than in any other lot.

This comparative study between staminate and pistillate plants, namely, quantitative increase of distillate (volatile oil) percentage of the weight of pollen, increased the percentage of staminate plants and decreased the percentage of pistillate plants. This seemed to be true for all the plants grown from seed which were obtained from the volatile oil sprayed pollen. On comparing the plants grown from the seed of lot *A*, portion 3 (pollen after 24 hours' exposure), with those of lot *C*, portion 3, pollen sprayed with distillate until it increased 60 per cent. of its weight, there is a difference of 26·1 per cent. In other words 26·1 per cent. more plants expressed maleness in their sex due to replacement of the original amount of volatile oils lost, plus a probable additional volume over the amount originally present in the pollen.

Evidently pollen from lot *A*, portion 3, was negatively affected by the decrease of volatile oil and pollen from lot *C*, portion 3, was positively affected by the increase of the oil with reference to the production of staminate plants.

Disregarding the number of non-blossoming plants, it was found that increase of staminate plants and decrease of pistillate plants due to this treatment (lot *C*) was still higher (29·0 per cent.) (see data in Columns XI and XII). It may be argued by some that this increase in favour of staminate plants and decrease in pistillate plants might be due to the addition of water rather than the volatile oil. The justification for such an argument would seem valid when one considers the data pertaining to lots *A* and *C*. In lot *A*, whereas volatile oil might have been decreased, water also evaporated.

Similarly in lot *C*, along with volatile oil, water was also added. The decrease of staminate plants might not be only due to the oil, but also due to water loss. Similarly the data showing increase of staminate plants due to increase of volatile oil might also be due to increase of the water content of the pollen. To decide this point we have the results in lot *D* where the same volume of distilled water for portions 1, 2 and 3 replaced the volatile oil. The data show that on varying the amount of water the ratio between the staminate and the pistillate plants remained practically the same. No particular increase of staminate plants was noted with the increase of water content, and this was also true of the pistillate plants.

We may, therefore, conclude that the increase in the proportion of staminate plants found in lot *C* was due in some way to the effect of the volatile oil on the pollen.

Summary.

1. The data show that a lower percentage of staminate plants is due to the lack of a proper amount of volatile oils left in the pollen before pollination.

2. By the use of pollen sprayed with volatile oil the percentage of staminate plants was increased by about 26·1 ± 1.

3. The data show that it is the presence or absence or abundance of volatile oil in the pollen which modifies the normal ratio of staminate and pistillate plants, and not the increase or decrease of water content. If water has any significance in the ratio, it is very small (± 4 per cent.).

4. It is possible by this method to increase the percentage of stami-

nate plants over that of pistillate ones, at least in the Mary Washington strain of asparagus.

To Messrs J. Van Tonningen and R. O. Cook of the California Packing Corporation, and to Mr Dorthy of the Sutter Basin Co., I wish to express my appreciation of the interest shown by them in these experiments. My thanks are also due to Dr Jones and Dr Bennett of the University of California.

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THE WHEAT SPECIES: A CRITIQUE.

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(With Fifteen Text-figures and Four Diagrams.)

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INTRODUCTION.

WHEAT genetics entered a fresh phase with Sakamura's discovery (1918) that the species might have 14, 28 or 42 chromosomes (diploid), and with Kihara's work on the cytology of hybrids between species with different numbers of chromosomes. Since then these partially sterile

hybrids have been studied by several workers both genetically and cytologically. In 1921 appeared Percival's account of the genus, in which the more important wheat forms from most regions of the globe were described and classified; and the work of Vavilov and his school, appearing chiefly from 1922 onwards, has still further enriched our knowledge of the systematics of the genus.

It must be confessed, however, that the various genetical and cytological workers have not always agreed in their conclusions, that this side of the work has proceeded almost independently of the systematics, and that it is difficult for workers on other genera to form an opinion on the various views put forward. It is, therefore, proposed to give in this paper, as far as possible, a critical account of what is known about the origin and genetic relationships of the wheat species, and of their behaviour when crossed. It is hoped that within the limits set no important questions of principle have been omitted, but no attempt has been made to deal with all the papers that have been published.

Two reviews of wheat literature have appeared recently: in 1927, Kajanus' "Die Ergebnisse der genetischen Weizenforschung"; and in 1928, Bleier's "Genetik und Cytologie teilweise und ganz steriler Getreidebastarde." The first deals primarily with the inheritance of the different characters. The second gives a descriptive account of hybrids in *Triticum*, *Secale* and *Aegilops*, their cytology, fertility and genetical behaviour when known. To both of these I am indebted for information.

In describing the species crosses we have to deal with plants possessing univalent chromosomes, and for these "haploid chromosome number" is a meaningless expression. I have therefore given diploid numbers throughout the paper, unless the contrary is stated.

I. SYSTEMATICS.

(1) Introduction.

The genus *Triticum* is nearly related to *Secale*, *Agropyrum* and *Aegilops*; and has indeed been united with the latter. To illustrate their relationship it may be mentioned that *Triticum* crosses readily with *Secale* and *Aegilops*, and that a tri-hybrid has been obtained by crossing an *Aegilops* × *Triticum* F_1 with *Secale cereale* (Leighty and Sando, 1927); and, again, that the wild grass *S. villosum* L. has also been described as *T. villosum* M. B.

At the present time *Aegilops*, which has been suggested as one of the

progenitors of *T. vulgare*, demands considerable attention; and for an account of the genus the work of Eig (1929) should be consulted. Its cytology has been incompletely studied, but it is worthy of note that there is no clear connection in this genus between chromosome number and systematic position, as there is in *Triticum*. The genus has been divided by Eig into several sections; the haploid numbers 7, 14 and 21 occur within both the sections *Pachystachys* and *Pleionathera*, while so far only the number 7 has been found within the section *Platystachys* (Schiemann, 1928 *a*, *b*; 1929).

(2) THE DIFFERENTIATION INTO THREE GROUPS.

In most genera of plants and animals insight into the problems of systematics is hindered because little is known about variation within species as they are found in nature; and *Triticum* is probably the only polymorphic genus of which it may be said that practically all types that now exist are known. Wheat is grown over the greater part of the world, ranging from about 67° N. latitude to almost tropical conditions. In North and South America, South Africa, and Australia, it has been introduced only in recent times, chiefly from Europe, and only a comparatively small number of forms are cultivated; but in the greater part of Europe, Northern Africa, and Asia, it has been cultivated from a very early period—in Europe it has been found in Stone Age deposits (Percival, 1921)—and, as we should expect from its antiquity and wide distribution, a great diversity of forms exists. Contrary to what might have been expected, wheat offers the same problems in systematics and geographical distribution that wild plants do. No doubt selection of seed, deliberate or automatic, has gone on from very early times; but, except in recent years in the most civilised countries, it has usually been done in crude and dilatory fashion, when done at all, and has not differed in principle from the selection exercised by nature. Similarly, the spread of new types seems usually to have been slow and continuous.

The list on p. 176 gives the species of the genus described by Percival in his monograph (1921), with the addition of *T. persicum*, a species recently described by Vavilov and Jakushkina (1925).

The first important point to discuss is this differentiation into three distinct groups of species with a different chromosome number characterising each group.

Most of the species and their diagnoses have been fairly well defined since the work of Seringe in 1841–2 (Percival, 1921); and the classification of Körnicke (1885) has only been superseded by the work of Percival

Group I	Group II	Group III
With 14 chromosomes	The "Emmer group" with 28 chromosomes	The "vulgare group" with 42 chromosomes
T. aegilopoides Bal. (wild form)	*T. dicoccoides* Körn. (wild form)	—
T. monococcum L.	*T. dicoccum* Schübl.	*T. vulgare* Host.
	T. persicum Vav.	*T. compactum* Host.
	T. orientale Perc.	*T. sphaerococcum* Perc.
	T. durum Desf.	*T. Spelta* L.
	T. polonicum L.	
	T. turgidum L.	
	T. pyramidale Perc.	

(1921) and of the Russian school. That the species fell naturally into three groups was concluded by Schulz in 1913 (see Tschermak, 1914; and Percival, 1921), by Vavilov (1914) as a result of studying their resistance or otherwise to the attacks of fungi; by Zade (1914) from serum reactions; and by Tschermak (1914) from the degree of sterility they show when crossed, a method amplified by Sax (1921). By Flaksberger (1915) and Percival (1921) this grouping was accepted.

Overton (1893) gave 8 as the haploid and 16 as the diploid chromosome number for *T. vulgare*; Körnicke (1896) reported the same numbers for *compactum*; while Dudley (1908), Nakao (1911) and Bally (1912) confirmed these results. Wheat is not easily fixed, and no doubt poor fixation was partly responsible for such a sequence of errors. However, Spillman (1912) stated that "wheat" had 40 or more chromosomes, and Sax (1918) found approximately 28 in the first division of the fertilised egg cell of *T. durum*. Correct counts were first given by Sakamura (1918), working with root tips, and finding 14 for *monococcum*, 28 for *dicoccum, durum, turgidum* and *polonicum*, 42 for *vulgare, compactum* and *Spelta*. He pointed out that these results agreed with the grouping of the species worked out by Schulz. Kihara (1919, 1921) confirmed Sakamura's numbers for the somatic cells, and found the corresponding haploid numbers, 7, 14, 21, at the reduction divisions in the microspore mother cells. These numbers are now well known, and there is no need to cite the numerous later workers who have confirmed them.

Nowadays it is sometimes the custom to settle the systematic position of a wheat form, if this gives difficulty, by counting the chromosomes. But it must be realised that the grouping of species was effected before their chromosome numbers were known; and Percival (1921) has described some 2000 forms which were all assigned to their appropriate species without knowledge of their chromosome number. It is, therefore, clear that there is a quite definite association between the chromosome

number of a wheat plant and its characters; and one of the problems before us is to discover the origin and reason of this association.

At this stage we may profitably ask what characters define the groups, and how great is the variation within each group. The differentiation into species will be dealt with later. Although such an enquiry would appear to be simple, it is, in fact, very difficult, for it soon becomes clear that it is far easier to recognise the group to which a previously unknown form belongs than to discover and describe the characteristics of such a group.

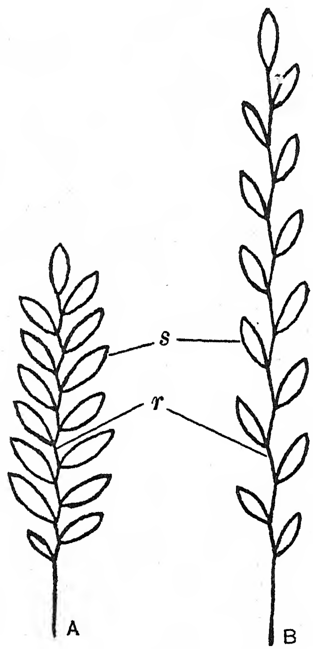


Fig. 1.

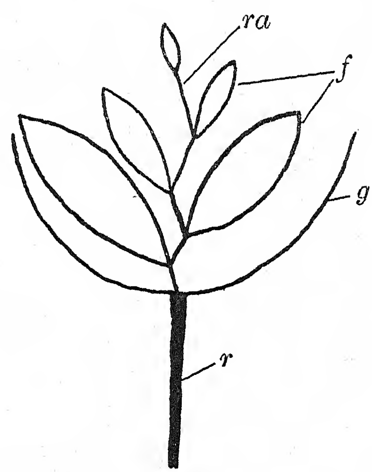


Fig. 2.

Fig. 1. Diagrams of ears of wheat in side view. A, dense ear; B, lax ear.
Fig. 2. Diagram of spikelet of wheat in face view. *r.* = rachis, *s.* = spikelet, *f.* = flower, *g.* = glume, *ra.* = rachilla.

Within the first group the range of variation is small and affects only a few characters. Relatively few types are known, and though it is possible that diversity was greater in the past, there is no doubt that this group, which is botanically the most primitive, is characterised by little variability. Both species are fairly easily recognised, and all forms have the primitive characters brittle rachis and tough glumes that invest the grains closely, while usually only one grain per spikelet is set.

In the second group diversity is great. Several hundred distinct forms are grown at Reading by Prof. Percival. Characters not found in the first group appear, such as rounded or weakly keeled glumes, loose glumes that do not hold the grain, tough rachis, many flowered spikelets, large grains, broad leaves and stouter straw. As many as 66 varying characters have been described by Orlov (1922) for the species *durum* alone.

But systematists are agreed that the greatest polymorphism occurs in the third group (Percival, 1921; Vavilov, 1922 *a*), and Prof. Percival grows more than a thousand forms yearly. Forms with beardless ears, with the straw almost devoid of pith, and with entirely different glume shapes, to mention only a few characters, appear for the first time. Evidently, as Sax has said (1922), there has been in the genus an increased variability with increased chromosome number.

Most characters vary in similar fashion within both the second and third groups; and some do so within all three. Of such characters several, such as colour of chaff, colour of grain, pubescence of chaff, have been shown to depend on one or more factors; and many others show no peculiar genetic features beyond those usually attributed, often prematurely perhaps, to characters dependent on a number of factors.

From comparing the variability of the groups we may turn to consider the characters by which they can be recognised. The 14 chromosome wheats (Percival, 1921; Flaksberger, 1925, 1926 *a*) have a striking general similarity, and differ from all other wheats by the palea, which divides longitudinally when the ear is ripe. They are also fairly easily recognised by the small grain, the ear shape, glume shape, and habit. The spikelets are two-flowered; and though in most types only one gives grain, both will set in most spikelets of "Engrain Double," a variety of *monococcum*. This variety, therefore, approaches *dicoccum* and *dicoccoides*, in which a set of two, or occasionally three, grains per spikelet is the rule (Percival, 1921). The fracturing of the rachis just above each spikelet when the ear is ripe is a character shared with *dicoccum* and *dicoccoides* alone; and the very slender straw is a feature sometimes found in the latter two species. Although quite clearly defined, the species of the first group evidently approach fairly closely to *dicoccoides* and *dicoccum*. Indeed confusion has occurred, for Flaksberger (1926 *a*) has shown that De Mol's count of 7 chromosomes (haploid) for *dicoccoides* (1924), instead of 14, was due to an incorrect diagnosis, the plant in question being really *T. aegilopoides* var. *Thaoudar*.

Separation of the second from the third group is more difficult, and

if we refer to Percival's description of the species (1921) we find only one character, the arrangement of the leaf hairs, with a definite constant difference in the two groups. To see the genetic problems of the species in their true light we must realise two facts: (1) that it is difficult to find any one character by which the two groups can be distinguished, and (2) that we can tell the chromosome number of any wheat from its appearance. The former point is well exemplified by the "Law of Homologous Series in Variation" enunciated by Vavilov (1922 *b*), largely as a result of his experience with wheat and other cereals; and we may conveniently consider his conclusions here. Parallel variation in allied species was mentioned by Darwin (1868) and other workers, and is

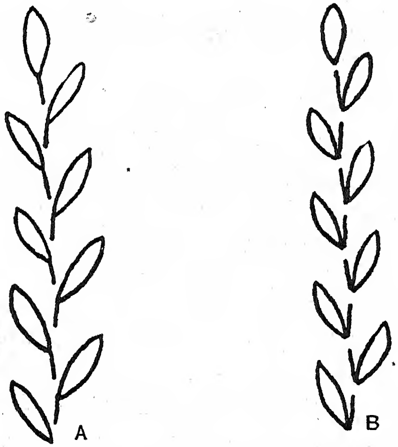


Fig. 3. Fracturing of the rachis. A, above each spikelet, as in *dicoccum*, etc.; B, below each spikelet, as in *Spelta*.

familiar to workers on Hymenoptera, Diptera and Lepidoptera; but it is to Vavilov that we owe the formal statement of the proposition and its application to practice. He states that the same alternative characters that distinguish the varieties of one species will also distinguish the varieties of other species of the same genus; and that a similar relation holds for the species of related genera. In "*T. durum, T. polonicum, T. turgidum*, there are white, red and black eared varieties, smooth hairy eared, white and red grained, winter and spring varieties" just as in *vulgare*. Again in rye, *Secale cereale*, just as in wheat, are found varieties with hairy or smooth ears, with hollow straw or solid straw, with a fragile or with a tough rachis, with ligules or without ligules, to quote a few out of 34 instances given. It was finding an eligulate wheat that led him to search for, and to find, an eligulate rye.

In the second and third wheat groups many characters vary; and the "Law of Homologous Series," pushed to its extreme conclusion, implies that no character that varies at all can be of diagnostic value, since it should vary equally in both groups. This conclusion is perhaps to a great extent true; and it is certainly very difficult to discover from the modern Russian systematic work, which is largely based on the Law in question, how the forms of these two wheat groups can be distinguished. It is perhaps a disadvantage of the theory that it has concentrated attention too much on resemblances between species, or groups, and not enough on differences, which from both the genetical and the practical standpoint are just as important. Of course the possibility remains that the groups are not distinguished by single characters but by the way in which the characters are combined, but this explanation is probably only partially true.

With this introduction we may consider in some detail the differences between the second and third groups.

Vavilov (1922 *a*) and Orlov (1922) describe 66 varying characters for the species *vulgare* and *durum* respectively. In most cases they are dealing with the same characters, so that it is not very difficult to compare the variation within the two species by examining their tables. In a few cases the characters are not comparable, but taking Vavilov's 66 as our standard we can summarise the results of the comparison as follows:

(1) 34 characters vary in the same way in both species.

I have included here the characters ligulate and eligulate; since eligulate *durum* forms have now been found (Flaksberger, 1926 *b*).

(2) In 6, *vulgare* has variants not given for *durum* but found in other 28 chromosome wheats.

Nos. 3, 9, 10, 14, 25, 34, in Vavilov's list.

(3) In 7 there are no differences of systematic importance.

Nos. 5, 29, 30, 45, 48, 63 and 66. Some of these are characters not dealt with by Orlov (*e.g.* variation in number of leaves, and in productivity), and in the others there is no important difference (*e.g.* the existence of purple grained *durum* forms is not important).

(4) In 6 the differences are probably, but not certainly, unimportant.

Nos. 20, 21, 35, 43, 50 and 55. The most important is the keel of the glume, for which the variation described in the two species is similar, and this character is given later in some detail. The others are not given by Orlov; an example is length of ear, a difficult character, but probably longer ears could be found among *vulgare* wheats than anywhere else.

Thus, out of 66 characters, no less than 53 vary in the same way in the two groups, or at the most show unimportant differences. Of the others:

(5) Five show a different, but overlapping, range of variation in the two cases and may be of systematic importance.

No. 8, hairiness of rachis, is not certain from the descriptions given; but probably differences do exist (cf. Percival, 1921).

No. 13, awn length, is not given by Orlov. Short awns may occur in either group but most *durum* forms have longer awns than are ever found in *vulgare*.

No. 38, habit of growth. Vavilov gives variation from erect to prostrate in *vulgare*; Orlov from erect to semi-erect in *durum*. Percival (1921) describes prostrate 28 chromosome plants, but the character is probably much rarer than in *vulgare*.

Nos. 40, solidity of straw, and 65, resistance to disease, are considered in detail later.

Probably some other characters would be found to belong to this class if they were examined in more detail.

(6) Eight show differences that are of some importance.

No. 1. *Vulgare* may be beardless or bearded, but 28 chromosome wheats are bearded except for occasional known hybrids.

Nos. 6, 15, 26, 31, 32 refer to shape of ear, of glumes, or of grains. Glume shape is dealt with later.

No. 42, leaf hairs. For both species variation from hairy to glabrous is described, but Percival (1921) describes differences in the way the hairs are arranged.

No. 36, grain hairs, is not given by Orlov. I am not familiar with this character, but important differences may exist.

The results, besides illustrating the Law of Homologous Series, show how difficult it is to find differences between the two groups. All the characters given were varying characters, and no invariable characters that would serve for differentiation have yet been discovered.

But though we cannot find a character that is common to all forms of one group and is quite absent from the other there are nevertheless characters that are confined to a single group though they are not common to all forms. The best example is perhaps *T. polonicum*, which has a very long glume, not found elsewhere in the genus, and is thereby easily recognised (Fig. 5 L). Other instances are: the beardless ears of many forms of the third group, though this character is easily transferred by crossing; brittleness of the rachis just above the spikelet, found only in *dicoccum*, *dicoccoides*, and to some extent perhaps in a few *durum* forms; brittleness of the rachis just below the spikelet, found only in *Spelta*; and other cases might be cited. Some characters, too, are developed to a greater degree in one group than in the other although there is no difference in kind: thus many *durum* forms have far longer awns than are ever found among 42 chromosome forms (Percival, 1921).

Further discussion may best be done by considering three characters: solidity of straw, resistance to disease, and glume shape.

Solidity of straw has already been noted (p. 181) as a character showing a different, but overlapping, range of variation in the two groups. Orlov (1922) describes *durum* as having straw that varies from hollow throughout to solid throughout; while *vulgare*, according to Vavilov (1922 *a*), varies from solid in the upper part to hollow (presumably throughout). But it would be far from the truth to suppose that the only difference was that variation in *vulgare* did not reach extreme solidity. In the first place the frequency of the different types is very different in the two groups. Thus the straws of most *vulgare* forms have little pith while those of most forms in the Emmer group are solid or half solid through a good part of their length (cf. Percival, 1921). Secondly, one cannot help suspecting that further differences would be revealed if the character were studied in greater detail. According to Russian writers (Orlov, 1922; Stoletova, 1925) some *durum* and *dicoccum* varieties have hollow straw; but no details are given, and the term "hollow" may perhaps be used in a comparative sense, so that one is tempted to ask whether the straw of any 28 chromosome wheat is quite hollow in the first few centimetres below the ear. It is certainly not in most of them, while, on the other hand, 42 chromosome wheats in which the straw is solid in this part must be rare. In *vulgare* the so-called solid strawed forms are fairly common in the Mediterranean region; but in these the distribution of the pith is quite different from that found in 28 chromosome forms, since the top internode is solid at the base and hollow at the top instead of the reverse being the case (Fig. 4). Although a careful study of the character is evidently wanted we can be sure that (1) completely solid straw is found only in the second group; (2) that hollow straw characterises most third group forms, and is rare, perhaps absent, in the second group; (3) that if the straw is partly solid in a third group form the pith is usually not distributed

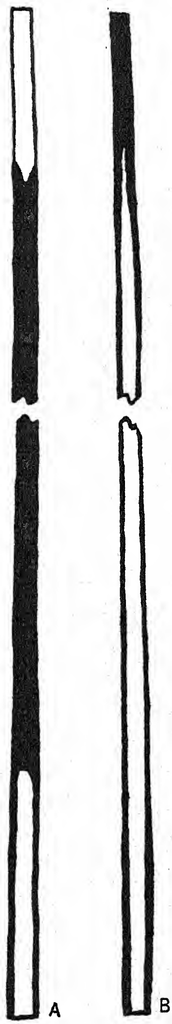


Fig. 4. Top internode of wheat straws. A, the commonest type of so-called solid strawed *vulgare*; B, a partly solid straw found commonly in 28 chromosome wheats.

as it is in second group forms. In the two groups the range of variation is different, and differences of a more fundamental kind may, perhaps, occur as well.

Disease resistance has been suggested by Vavilov (1914) as a test in systematics, not only for cereals but for other plants. He did not suggest an invariable association between resistance or susceptibility and systematic position, but since his work the idea has gained ground that all second group forms are resistant or fairly resistant to rust and that all third group forms are, in differing degrees, susceptible. This belief has come about not only from the reactions of the better known varieties but also because it is difficult to transfer, by crossing, the resistance of a 28 chromosome form to a susceptible 42 chromosome form. Vavilov (1922 *a*) describes *vulgare* as either resistant or susceptible to *P. glumarum*, *graminis* and *triticina*; Stoletova (1925) gives the same description for *dicoccum*; while Orlov (1922) gives *durum* as resistant or "feebly subject" to *graminis*. The question is not an easy one. Difficulties are inevitable when we try to study the inter-relation of two separate organisms; and in *graminis*, if not in the other species of rust, an added complication is the existence of a number of biologic forms, each reacting differently to different varieties. In the case of *P. glumarum* it is probably correct to say that the majority of forms in the second group are moderately or completely resistant, a few being susceptible, while the majority of third group forms are moderately or very susceptible, a few only being resistant. If Prof. Percival's wheat collection is examined it is very striking that nearly every variety that is yellow with rust is a 42 chromosome form—very few have 28 chromosomes. Although *T. compactum* var. "American Club" ($2x = 42$) has always been immune at Cambridge, such instances are rare; and most of the so-called resistant third group forms are attacked to some extent when the rust epidemic is severe. Almost complete resistance is common, however, among second group forms and, as we have seen, great susceptibility is not. Resistance to *glumarum* appears to be an example of a character that has approximately an equal range of variation within the two groups, but high resistance is commonest in the second group and low resistance, that is high susceptibility, in the third. In the case of *graminis*, biologic strains are an added complication; but probably the situation is not very different from that in *glumarum*.

Finally, glume shape must be dealt with. This is probably more important in wheat systematics than any other character, and indeed one could probably tell the chromosome number of any wheat form by

examining the glume alone. But it is a most difficult character to discuss, not only because it is difficult to define and describe shape, but also because it is often difficult to know exactly upon what features recognition is based even when the recognition itself is quite certain. At one time it was thought that wheats of the second group could be distinguished from those of the third by the presence of a keel to the glume, but it is now known that this feature is quite well developed in a number of *vulgare* forms, *e.g.* from Persia and Bokhara, as well as in speltoids. For *vulgare* Vavilov (1922 *a*) describes the keel as "sharply prominent" or "not prominent," and for *durum* Orlov (1922) gives it

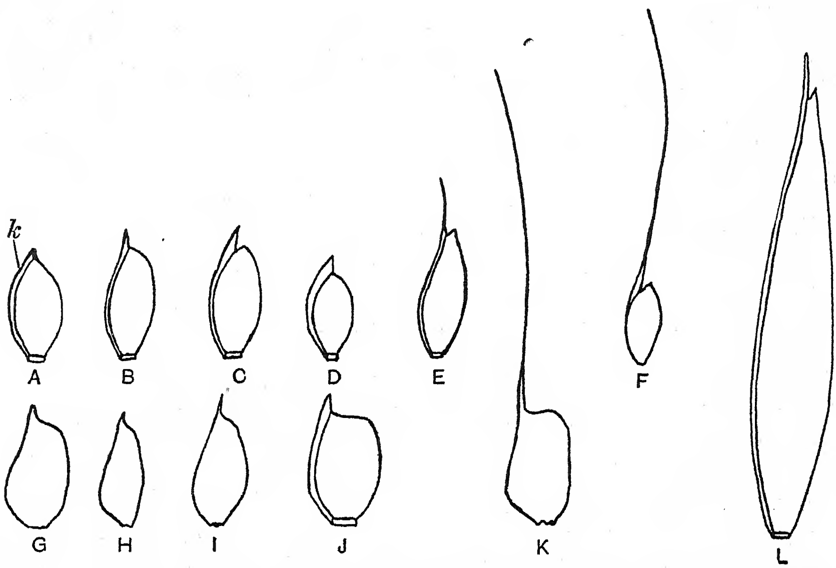


Fig. 5. Outlines of glumes. A–E, *durum* and *turgidum*; F, *persicum*; G–K, *vulgare*; L, *polonicum*. The difference between the keeled and keelless forms is somewhat accentuated. *k*=keel.

as well developed from the top to the base or feebly developed at the base. In the 28 chromosome *T. persicum* it is only weakly developed. In fact, though the character is important, it is so only when considered in relation to other glume characters as well; and there is no doubt that glumes are recognised by the way in which their characters are combined, as must be the case when recognition is based on shape. In dealing with shape it is very difficult to know what should be regarded as a unit character, so that discussion from the genetical standpoint is not easy, and it is doubtful whether any useful purpose would be served by trying to describe such characters here; especially as no adequate study of

variation in glume shape has been attempted in the genus. It should be realised, however, that glume shape is often very characteristic. Thus the type of the Northern European beardless *vulgare* (Fig. 5 G) is different from anything found among 28 chromosome wheats, nor is the typical broadly keeled *turgidum* or *durum* glume ever seen among those with 42 chromosomes. It is probable that linkage plays an important part in the genetical relationships. Thus Percival's statement (1921) in describing the glume of *vulgare* as terminating "in a tooth, which in the beardless forms is short and usually blunter than that of *T. durum*, and in the bearded form often prolonged into a slender awn," suggests the possibility that either the factor for awns, or another factor linked to it, modifies the length of the glume tooth; and since all 28 chromosome wheats are beardless, while third group wheats may be bearded or beardless, this would clearly be important.

We may sum up by saying that the wheat species fall into three clearly defined groups, each with a different chromosome number, and that the chromosome number of any wheat form can be told from inspection. The situation is quite different from that in *Primula sinensis* for example, where the tetraploid is clearly only a form of the species *sinensis*, and is in no sense a distinct species. But it is difficult to say exactly how the three groups, particularly the second and third, are characterised; and from the point of view of the genetical worker this problem, which is of first importance to him, has been insufficiently studied. The Law of Homologous Series, while undoubtedly valuable in many other ways, has withdrawn attention from the question. Nevertheless, considering the most difficult case of the second and third groups, we have at any rate learned that a few characters are found only in certain forms of one or the other group, and that a few types—as *dicoccum*, *polonicum* and *Spelta*—are thereby recognised. Secondly, it appears that although some characters may vary within both groups, the two extremes of variation are either entirely confined to, or are found most often in, different groups. At the same time, the examples that were given, solidity of straw and resistance to disease, suggested that further study of such cases is to be desired. Thirdly, in the case of glume shape, classification depends on the way in which characters are combined.

To give a concrete example, it might be thought that, since both solid straw and rust resistance are common in the second group and are rare in the third, the chance of finding a rust resistant *vulgare* wheat with solid straw would be very small indeed, and that by examining a new form for several such characters identification of the group to which it belonged

would be almost certain. Actually this is wrong; since, perhaps because of genetic linkage, the two characters cited are not independent. Vavilov (1922 *a*) says that solidity of straw is a "rare feature to be found only in a comparatively small group of races of soft [*i.e. vulgare*] wheats.... This feature is, as a rule, accompanied by a series of others, such as immunity to parasitic fungi or peculiarities in the structure of spikes." Nevertheless, although the problem in question has not been solved, enough has been learned for us to appreciate the genetical results, and further discussion will be deferred until they have been dealt with.

The difficulty we have had in defining accurately the wheat groups is probably typical of the classification of any polymorphic group of plants.

(3) The differentiation into species.

Differentiation within the groups is a distinct problem from that of differentiation into the groups themselves, there being no changes in chromosome number and no sharp lines of separation in many cases.

In the following account of the species I have sometimes referred to their distribution in prehistoric times, but too much reliance must not be placed on what is said. There is no doubt that a great deal of valuable material has been obtained in the past, but identification has often been left to those with little knowledge of wheat, and in many cases a sample has been described merely as "wheat" with no mention of the species. For preference, glumes should be present in the sample to assist identification; but in most cases these, even if present, are broken up during excavation and only the grains are left. To identify the species from the grain alone is a matter for those with special knowledge. Even so mistakes are easy, chiefly because little is known about the changes in grain shape that might have been brought about by carbonisation, and partly perhaps because possible changes in the species since prehistoric times might make identification uncertain by modern standards of difference. References to most of the work done can be found in Percival's monograph (1921) but it should be realised that in great part the conclusions of the earlier workers are probably wrong; though the identification of *T. dicoccum* Schrk. by spikelets should usually be correct. It is to be hoped that, in the future, more attention will be paid to these matters by archaeologists, since valuable knowledge could thus be won about the origin of wheat and the spread of early civilisations.

The first group contains only two species: *monococcum* (cultivated) and *aegilopoides* (wild). Both are peculiar to mountains, and are found chiefly 700 metres or more above sea-level (Flaksberger, 1925).

T. aegilopoides Perc. (= *T. monococcum aegilops* Asch. and Gr.). "Wild einkorn" is found in the area from the Balkans to Syria and Transcaucasia (Percival, 1921; Flaksberger, 1925, 1926 *a*). In the Balaklava district it occurs in a community composed of *Festuca ovina*, *Aegilops cylindrica*, *A. ovata*, and other plants (Drosdow, 1923). Flaksberger (1925) divides the species into two sections: (1) a two-awned Asiatic race, var. *Thaoudar*, confused by de Mol (1924) with *dicoccoides*; (2) one-awned forms, comprising 10 varieties. Percival (1921), who regards leaf-hair arrangement as a very important character, describes the same arrangement for *aegilopoides* as for *vulgare*, and a quite different one for *monococcum* and for all second group species. The rachis of *aegilopoides*, like that of *dicoccoides*, is far more fragile than the rachis of the cultivated species *monococcum* and *dicoccum*.

T. monococcum L. This differs from *aegilopoides* in ear shape, glume shape, size of grain, and shorter awns (Percival, 1921), and, though similar, is not likely to be confused with it. It is cultivated in scattered localities in mountainous districts in Europe; chiefly in France, Spain, Switzerland, the Balkans, and the Crimea (Percival, 1921; Flaksberger, 1925). Flaksberger (1925) describes nine varieties. The diversity of the species is small, affecting principally characters such as glume colour. On botanical grounds it is believed to be the most primitive cultivated wheat, and is said to have been widely cultivated in parts of Europe in Neolithic times.

In the second group Percival (1921) recognises seven species: *dicoccoides*, *dicoccum*, *orientale*, *durum*, *polonicum*, *turgidum* and *pyramidale*, of which two—*pyramidale* and *orientale*—are new species separated from *durum*. Vavilov (1925) describes an eighth species *persicum*, established originally on a single variety "Black Persian" which Percival has included within *T. dicoccum* Schübl. In general it may be said that, when crossed with one another, all these species give fully fertile hybrids; though a possible exception is *dicoccoides* (Vavilov, 1926), which is said to show a marked tendency to sterility in crosses with other 28 chromosome wheats[1]. In several cases it is difficult to separate one species from another, and Kajanus (1927) has proposed to unite them as a single species *T. acuminatum*.

T. dicoccoides Perc. (= *T. dicoccum dicoccoides* Körn.). "Wild Emmer" is found from Palestine to Transcaucasia. In Palestine it is found in some diversity; varying chiefly in the shape of the spikelet, shape of the tooth of the empty glume, hairiness of the rachis, colour of glumes and awns (Percival, 1921; Flaksberger, 1926 *a*). According to

[1] In my own experience, with several crosses, this is not the case.

Percival it is easily separated from *dicoccum* by a number of characters, such as exceptionally brittle and hairy rachis. It has usually been regarded as the wild form of *dicoccum*, and hence as the progenitor of all the cultivated wheats. Flaksberger, however (1926 *a*), considers it more like *Thaoudar* and *aegilopoides* than like *dicoccum*, except for its chromosome number and not-splitting palea, and finds it "difficult to consider it as the initial form or progenitor of cultivated Emmers, though their relationship must be recognised."

Two descriptions of *dicoccum* are known: *T. dicoccum* Schübl. described by Percival, and *T. dicoccum* Schrk. as more usually recognised.

T. dicoccum Schrk. (Emmer) has tough glumes and a brittle rachis which breaks just above each spikelet—characters it shares with the 14 chromosome wheats and with the wild *dicoccoides*. Typically it sets only two grains per spikelet, but a number of varieties set three under good conditions of cultivation. It shows the usual variation in colour of glumes and awns, etc.; and in addition varies in glume shape, solidity of straw, and resistance to the various rusts (Percival, 1921; Stoletova, 1925). Vavilov (1926) says that in Abyssinia "easily thrashed emmers were found (H. Harlan)," but I know no further details of these. It is, however, a species well defined by the characters given above, and to some extent by its vegetative characters, and is not likely to be confused with any other. It is one of the most primitive cereals, and is now cultivated only by "ancient peoples who stick to their secular customs and traditions" (Stoletova, 1925; and, similarly, Percival, 1921). The acreage under Emmer is at present gradually diminishing.

T. dicoccum Schübl., as described by Percival, includes (1) *T. dicoccum* Schrk., (2) a number of Abyssinian wheats with a tough rachis and loose glumes classed by other workers as *durum*, (3) "Black Persian," *i.e. T. persicum* Vav., regarded by Percival as very similar to one of the forms of (2). His justification for this grouping is that "Black Persian" and the Abyssinian forms with a tough, or semi-tough, rachis resemble the Abyssinian examples of *dicoccum* Schrk. in having from 3–6 vascular bundles in the coleoptile, whereas all other wheats have 2 (Percival, 1927); again, in having the young leaves more or less covered with short hairs, like *dicoccum* Schrk. and unlike *durum*; while the slender rachis of many forms confirms this grouping in many cases.

In its various forms *T. durum* Desf. approaches closely all the other species in the 28 chromosome group, of which it is the most diverse member. Its limits are not well defined, and authorities differ as to its exact definition. Thus Orlov (1922) includes in this species *T. pyramidale*

Perc., *T. orientale* Perc., and the Abyssinian forms with tough rachis and loose glumes from *T. dicoccum* Schübl. Typically it has a sharply keeled, loose glume, a tough rachis, and hard flinty grain; but difficulty arises, to take only one example, with forms that have a half flinty, half mealy grain, and so approach the mealy grained *turgidum*. Percival (1921) describes the species as characterised by having no hairs on the upper surface of the young leaves which, in the other 28 chromosome wheats, are densely clothed with short hairs; but here again, transition forms, considered by Percival as hybrids, can be found moderately or very sparsely clad with hairs. We may well quote Orlov (1922) here: "The polymorphism of *Tr. durum* is very great. The range of its race characters is exceedingly extensive. Races, with characters expressed in an extreme degree, are met with rather seldom. The nearer the character to its medial expression, the more such races are found. They are predominant botanical forms, building the ground to the polymorphism of the species *Tr. durum*..." constituting "the fundamental typical form...around which are grouped all the other races."

T. polonicum L. is easily recognised by its very long glumes, ribbed and papery in texture, and by its very long grains. All these differences have been found by Biffen (1905) and Engledow (1920) to be due to a single factor difference from *durum*, to which the species is closely related. Bateson (1926) suggested that so many characters were probably due to a group of completely linked factors, and this is supported by an Abyssinian race, grown by Prof. Percival, which is typical *polonicum*, except for its short grains. The converse, a *durum* with grains as long as *polonicum*, is widely spread in the Mediterranean region.

T. turgidum L., though connected with *durum* by transitional forms, comprises a fairly well-defined group, tall and late in ripening, with mealy grains and leaves abundantly covered with soft hairs.

T. orientale Perc. comprises a few forms having affinities with *dicoccum* Schübl. and *durum*.

T. pyramidale Perc. consists of a few forms from Egypt related to *turgidum*, but differing from the latter in the short straw, earliness, and one or two other features.

T. persicum Vav. In 1914 Vavilov found that "Black Persian," which was then referred to *T. vulgare* var. *fuliginosum* Al., differed from all other wheats tested by him in being immune to *Erisyphe graminis*. Percival (1921), from its leaf hairs arrangement, partially solid straw, slender rachis, and the number of vascular bundles in the coleoptile, brought it to *T. dicoccum* Schübl. This affords a good illustration of the

connection in *Triticum* between chromosome number and systematic position, since the variety is now known to have 28 chromosomes. Its original inclusion within *vulgare* is clearly wrong when it is carefully examined, and rested largely on its rounded glumes, most second group wheats having more or less strongly keeled glumes. The original seed came from Haage and Schmidt who had no record of its origin except that it might have come from Persia. Vavilov (1926) could not find it in Persia but suggested that it should be considered a separate species, *T. persicum*, in the Emmer group. Zhukovsky (1923), Atabekov (1925) and Dekaprilevich (1925), found it in some diversity in Central Transcaucasia, mountainous Armenia, and Georgia. Its separate distribution confirms Vavilov's view that it should be classed apart from the other 28 chromosome species.

This survey of the second group brings out certain facts quite clearly. First, a number of new characters appear which were not found in the first group, and with them has come much greater diversity. Secondly, the species are connected with one another by transitional forms, and no general agreement as to their exact definition has been reached. While deferring for the moment a fuller discussion, we can conclude that the problem is the origin of a large number of forms, all more or less connected, and not sharply separated into species; but definitely clustered round a number of fixed points, which are the "typical forms" of the systematist's species.

The species of the third group—*vulgare, compactum, sphaerococcum, Spelta*—are easily defined, and there is no disagreement as to their limits. But the differences between them are small, and when crossed they give fully fertile hybrids apparently showing simple Mendelian segregation, so that Kajanus (1927) has proposed that all should be brought to one species *T. obtusatum* Kaj. No wild 42 chromosome wheat is known.

T. Spelta L. is separated from all other wheats by its tough glumes and brittle rachis breaking just below each spikelet; the grains being rather long and pointed with a ridge along the dorsal surface due to pressure of the glume. Otherwise it is like typical *vulgare* in its hollow straw, broad rachis, rust resistance, etc. It is cultivated only in scattered patches in Europe (Percival, 1921) and in N.W. Persia (Vavilov, 1926), and is regarded by Vavilov as a relict. In its ear characters, tough glumes and brittle rachis, it differs from *vulgare* by one factor (Kajanus, 1923 *a*; Nilsson-Leissner, 1925; and others), and carries in addition an independent factor that produces very dense ears in *vulgare*; but the genetics of the longer grain are not known.

T. compactum Host. differs from *vulgare* only in its very dense club-shaped ear, and its rounded grains. The ear difference was found by Nilsson-Ehle (1911) to be due to only a single factor.

T. sphaerococcum Perc., while having the general characters of *vulgare*, is well defined by its short straw, very small and rounded grain, and its small and characteristically shaped ear. No account of its genetic difference from *vulgare* has been given.

T. vulgare Vill. is the most diverse species in the genus. Over 1300 varieties are grown yearly by Percival; while Vavilov (1922 *a*) says "at present, the author distinguishes races by 66 fundamental characters, the number of which, with their subdivisions, reaches 166"; and later "The greater number of the characters...are quite independent and admit of all kinds of combinations." False ideas as to the characteristics of the species, so often seen in past systematic work and in modern genetical writings, have come from the limited range of forms grown in Northern Europe and in America. No difficulty is likely to arise about separation from the other species in the group, which comprise only a few forms with their special characteristics; and the separation of the whole diversity of *vulgare* from the second group forms, for which familiarity with the types is necessary, has been discussed already. The species as a whole has been divided into several sections. Flaksberger (1915) recognises six, Percival (1921) seven, and Vavilov (1922 *a*) three (or four, including the square-headed wheats). To some extent the groups of the different authors coincide; and all have, more or less, their own geographical distribution. Thus Vavilov's group *rigidum* corresponds to Percival's group I, and is peculiar to S.W. Asia; his group *Speltiforme*, peculiar to the same region, corresponds to Percival's group III; and his *Indo-europaeum* to Percival's groups V and VI (Vavilov, 1922 *a*). It is not likely that there would ever be general agreement as to the limits of these groups, which no doubt overlap; but it seems possible that here, as in the second group, though probably less definitely, the different forms are clustered more thickly round some points than round others.

Percival (1921) cites several authors as identifying samples of Neolithic age as *vulgare*; but all these earlier identifications may be wrong.

Further classification depends upon the division of species into botanical varieties. The various systems (Flaksberger, 1915; Percival, 1921; Vavilov, 1922 *a*) are based on a number of easily recognised alternative characters, such as presence or absence of awns, colour of

chaff, and so on. Thus *T. vulgare* var. *lutescens* Körn. means any beardless, red grained *vulgare* wheat with smooth, white chaff. As Vavilov says (1922 *a*), "Two forms belonging to two different botanical varieties, for instance to *T. ferrugineum* Al. and *T. erythrospermum* Körn., might be different in only one hereditary factor—the colouring of the head; but it would be possible to find for instance within the limits of var. *graecum* two races (Jordanons) which differ from each other at least in 20 various morphological and physiological features." The system is purely one of convenience in cataloguing, and has no natural basis.

We have now surveyed briefly the systematic position in *Triticum*; and the ultimate aim of the genetical worker must be to explain the distribution of characters, and their combinations, throughout the genus. One essential for this purpose is a more accurate definition of characters than has so far been achieved. Apart from its theoretical interest, the Law of Homologous Series gives a convenient method of classifying variations, and has helped in the search for new forms. But by concentrating attention on the similarity between species it has led to neglect of their differences; and by describing characters as merely alternative we are led to overlook the fact that range of variation may be different in two species. Probably greater accuracy will have to come largely from genetical work, since it is likely that no character can be accurately defined until its inheritance has been worked out in Mendelian terms.

(4) Reproduction in wheat.

Wheat is described as a self fertilised plant; and crossing certainly appears to be uncommon in Northern Europe (cf. Fruwirth, 1923). Nevertheless, it does occur, and we must know something of its extent before we can understand the systematics of the genus.

To prove a natural cross may sometimes need careful observation; and although it may be true that no certain case of factor mutation has been found in wheat, it is hardly logical, without further proof, to dismiss every spontaneous variation as a natural cross. We may recall that the origin of fatuoid oats, once attributed to natural crossing, is now known to be due to chromosome aberration (Huskins, 1927). But we can be fairly certain of a natural cross if we can observe the introduction of two independently segregating characters; and it is sometimes possible actually to identify the pollen parent when the segregation is observed. Some of the instances given below are unreliable judged by this standard, but may be accepted in view of the more certain cases.

At Cambridge crossing has always been regarded as rare, but has been

found to occur quite often in partially sterile hybrids which set grain irregularly with their own pollen and leave the ovules more open to out-pollination (Watkins, 1925). Varieties that set grain badly in the English climate are also specially liable to crossing, and in the last few years several instances have been found between normal English varieties grown close together in small plots. It is important to notice that in all these cases the pollen parent has been in a neighbouring plot not more than a few yards distant. At Reading, where some thousand varieties are grown side by side, many examples have been seen (Percival, 1921), but no doubt exotic forms unsuited to English conditions are partly responsible. In America, Hayes (1918) and Leighty and Taylor (1927) have shown that crossing may sometimes be fairly frequent. Here, again, the pollen parents appear to have been plants from neighbouring plots. We must remember, however, that field crops are not necessarily comparable with the small plots grown at experiment stations, where exotic varieties will exaggerate the importance of natural crossing. On the other hand, since out-pollination appears to be usual only between neighbouring plants, it should be more frequent when a very mixed crop is grown in the field than when a number of pure varieties are grown in adjacent plots. Under English conditions, in times when crops were more mixed than now, it evidently occurred not infrequently since Le Couteur (1836), at Jersey, records an ear with rough red chaff that gave rough red, smooth red, rough white, and smooth white progeny. It is known that natural crossing is more frequent in hot climates, and here its importance must be all the greater since in these regions very mixed crops are commonly cultivated. The Howards (1910), who have paid special attention to the subject, found that three ears collected from cultivator's fields in Bihar were natural crosses; and in one year at Lyallpur, where a collection of Indian wheats was grown and the frequency therefore perhaps exaggerated, 226 instances were found—some of them involving two or three characters. In Mesopotamia, too, Wimshurst (1920) suggests that natural crossing is frequent, and from Abyssinia I have myself received an ear that proved to be F_1 between *polonicum* and some other 28 chromosome wheat. Under modern civilised conditions, where comparatively pure crops are grown, out-pollination would be less important, and in any case its effects are counterbalanced by continuous selection of seed; but nearly everywhere else—and a hundred years ago even in civilised countries—selection of seed was often almost non-existent, and even occasional out-pollinations would have a profound effect when long continued.

Enough has been said to show that natural crossing must have had considerable influence in forming the many combinations that exist in wheat, and its part in evolution should be reconsidered. At present something must be said of its limitations.

Apart from the obvious limitations imposed by geographical distribution there are those set by date of flowering, ease of crossing, and sterility. The latter operates only in inter-group crosses, and personally I doubt whether such crosses have had much influence on the genus, though the contrary is often suggested—usually on rather uncertain morphological grounds. Thus Vavilov, speaking of the awnless European square headed *vulgare* wheats (1922 *a*), says: "Their weak winter resistance and usual immunity to yellow rust suggest that besides *T. vulgare* and *T. compactum*, *T. turgidum* had a share in their origin too"; and again (1926) he speaks of *persicum* as occupying an intermediate position between the second and third groups, and probably originating from a cross between them. Similar views are often expressed, but it should be noticed, and the case is I believe typical of most others, that the comparative resistance of the square-headed wheats to *P. glumarum* is given as a reason for *turgidum* being a progenitor; and it is precisely characters such as resistance to disease which all genetical writers agree can only be transferred from one group to the other with great difficulty. Positive evidence against attaching much importance to crosses between different groups lies in the almost complete absence of beardless 28 chromosome wheats, despite the fact that beardlessness is a common *vulgare* character found over a great part of the range of the second group wheats, and readily transferred from *vulgare* by artificial crossing, giving fully fertile 28 chromosome segregates. Whatever the reason for this may be it suggests that crossing between the two groups has done little to increase their diversity. But from what has been said I think we can conclude that natural crossing within the groups has had considerable influence in diversifying types.

(5) Selection.

Wherever wheat is grown natural selection will ensure that only forms that are more or less suited to the prevailing climate and methods of cultivation will be grown. Of India, Howard (1909) says: "The wheats at present in cultivation in this vast empire, in which a civilised agriculture has been practised from time immemorial, represent the survival of types most fitted for the conditions of the various tracts.

Nature has eliminated the unfit"; and he adds that no new forms have had any influence, at any rate in recent times.

Except for highly civilised countries in recent years, selection by man has probably always been slow and sporadic; and we find that fields of wheat consist, in greater or less degree, of a mixture of varieties. In England at the present day crops are often far from pure, and less than a century ago they must have been badly mixed. Le Couteur, who provided us with the first historical case of breeding on the pure line principle, when telling how he was first led to breed wheat by La Gasca, says: "I considered" my crops "as pure, at least as unmixed, as those of my neighbours, when to my dismay he drew from the fields three and twenty sorts. Some were white, some red, some liver-coloured, some spring-wheat, some dead ripe,...and some green" (1836, p. 115). Nowadays in backward countries the situation is usually not different from that found in India, where "An examination of an ordinary wheat field...at harvest time discloses the fact that the crop consists of a mixture of botanically different varieties sometimes belonging to two or three sub-species" (Howard, 1909), and samples obtained from such countries may yield an extraordinary mixture of types when sown. Often, practically no attention is paid to seed selection. In Oudh the poor cultivators go to dealers for seed, when "inferior wheat is often given for this purpose with the result that in the course of time the Oudh wheats are said to have greatly deteriorated" (Howard, 1909). Similar practices are widespread, but greater care is sometimes taken, the practice varying largely according to the wealth of the district and the importance of the wheat crop: in the Punjab "the best cultivators keep their own seed and in some cases select the ears in the field for sowing the next crop" (Howard, 1909); in Mesopotamia, in the area of Hai and Shatt el Ghurraf, "more attention would appear to be paid to seed selection and wonderfully pure crops...were met with" (Wimshurst, 1920).

In Roman times mass selection for the largest ears or the largest grains was sometimes practised (Percival, 1921). Other examples could also be given.

We may probably take it that from the earliest times, though most cultivators have had little interest in the type of wheat they grow, there has been in some of the more prosperous districts a crude but long-continued selection for characters of obvious utility such as size of ear or grain, and to this must be attributed the excellence of the types often grown in such districts. No doubt the advantage of a wheat with loose

glumes and a tough rachis, in place of *dicoccum* with its tough glumes and brittle rachis, would be readily recognised when such a type appeared. But the continued cultivation of *dicoccum* by primitive tribes shows how slowly changes came; and it is safe to assume that botanical characters have been almost neglected, and that newly risen characters have spread slowly and by chance with the introduction of seed to new districts. Occasionally a botanical character may have an accidental economic importance, but this does not always make much difference. Thus, in many hot countries, bearded are said to be preferred to beardless varieties because less loss is suffered from birds and from shedding in dry weather; but this does not seem to have prevented beardless forms from being widespread in such countries.

For these reasons the problems of evolution and geographical distribution in wheat and in wild plants appear to be similar in principle. This is clearly illustrated by the regularity in geographical distribution found by Vavilov. In the Old World "in spite of the internationalisation of cultivated plants, the wanderings of the peoples, in spite of colonisation and the antiquity of agriculture, it is still possible to establish...areas of definite endemic varieties and races, regions displaying a maximal primary diversity of varieties, and to find out series of regularities in the distribution of these varieties" (Vavilov, 1926). Local needs may have their influence, but the general scheme remains.

(6) Theories of origin.

Past speculations on the origin of wheat were for the most part founded on too little knowledge, and will not be here discussed. Modern theories to be considered are three: that of Percival (1921) founded on systematic data; Vavilov's conclusion (1926) from his work on geographical distribution; and Winge's (1917) theory of the origin of polyploid series.

Percival takes the three groups separately. In the first group the relation between the wild *aegilopoides* and the cultivated *monococcum* is regarded as evident, the only modification in the latter being "a reduction in the hairs on the leaves and rachis."

The problem of the second group species is thought to be similar. "Crossing between mutants of the same specific prototype is, I think, sufficient to account for many, if not all, of the moderate number of forms found among the races of the Emmer series." *Dicoccum* and *orientale* are supposed to have come from *dicoccoides*, on the ground of their similarity to that species and of their differing from it only by the

absence or modification of its characters. Similarly *durum* is supposed to have come from *dicoccoides* or *dicoccum*, and *polonicum* from *durum*. On the other hand, *turgidum* is considered "a hybrid race produced... by the crossing of the tall European *T. dicoccum* with *T. compactum* or a dense-eared form of *T. vulgare*," a number of characters showing its affinity to European Emmer, while the square ear, many flowered spikelets, and plump, blunt-ended grain are thought to be derived from *compactum* or *vulgare*.

In the third group "the extraordinary complexity and almost endless number of varieties and intermediate forms of the *vulgare* race can only be satisfactorily explained by the assumption of its hybrid origin from two or more distinct species." It is concluded that, to explain the origin of *vulgare*, we must account for the following characters which differentiate it from the 28 chromosome forms: (1) leaf hair arrangement, (2) hollow straw, (3) exceptionally tough rachis, (4) the rounded back and absence of keel on the lower part of the glumes of most forms, (5) the short awns of the fully bearded ears, and the beardless and semi-bearded ears. Since all these characters are found in *Aegilops ovata* L. or *A. cylindrica* Host., it is concluded that both these species have entered into the composition of *T. vulgare*; while "the greater length of ear, frequently keeled empty glume, larger grain, and occasional solid culm" are thought to point to *dicoccoides* or one of its derivatives as the other parent. *Vulgare*, then, is thought to come from crosses between a 28 chromosome wheat and *A. ovata* and *cylindrica*; while *Spelta* is thought to be a segregate from this hybrid, and to derive its brittle rachis from *A. cylindrica*. *T. compactum* and *T. sphaerococcum* are regarded as having originated contemporaneously with *vulgare*, either as mutants, or as segregates from crosses between different *vulgare* wheats.

Vavilov (1926) has shown that wheat, and other cultivated plants, have definite centres of diversity—regions where the greatest number of types are found—and that as we leave these centres the number of types gets fewer. Apart from *T. dicoccum* Schrk., for which the existing data are too scanty, he finds that all 28 chromosome species except *persicum* have their maximum diversity round the coasts of the Mediterranean and in Abyssinia; in which regions a "multitude of original and endemic forms," as well as all varietal characters of European and Asiatic forms, are found. On leaving these centres fewer and fewer forms occur. On the other hand, the 42 chromosome *vulgare* is most diverse in Persia, Afghanistan, mountainous Bokhara, West India, and Kashmir, where, in addition to common European and Siberian forms, there are many

endemic varieties as, for instance, forms without ligules. *Sphaerococcum* occurs in Northern India only; and the greatest diversity of *compactum* is in Khiva and on the borders of North West India.

In accordance with the usual principles it is assumed that these centres of diversity are the centres of origin. All early writers on wheat took it for granted that cultivated wheats had a single origin but, agreeably with modern cytological and genetical work, the botanico-geographical method shows three distinct centres. *Vulgare* probably originated in Eastern Afghanistan, and the other 42 chromosome species in neighbouring regions: the 28 chromosome species in the Mediterranean region or the mountains of Abyssinia: and the 14 chromosome forms probably in the region of Asia Minor, though data for these wheats is rather scanty. As Vavilov points out, the assumption that the centre of diversity is really the centre of origin evidently agrees with the data. In Afghanistan, which is the centre for 42 chromosome wheats, and where conditions vary from sub-tropical to the limits of agriculture in the mountains, there are no forms at all of *durum* or *dicoccum*, which are common and very diverse in mountainous Abyssinia. On the other hand, no great diversity is found in the Alps or the Pyrenees.

The general truth of Vavilov's contention must be granted, but it must be admitted that the present centre of diversity may not quite coincide, perhaps, with the original centre of origin. How far may a regularity in the wanderings of peoples have contributed to a regularity in the distribution of wheats? Vavilov finds (1929) that, besides *T. vulgare*, a number of other cultivated plants have their greatest diversity in Afghanistan, and this inevitably suggests that the oft recurring migrations of peoples through Afghanistan into India may be the reason. Indeed the collector of Indian coins finds that their diversity increases as Afghanistan is approached; and no doubt any form that might be introduced would have a good chance of surviving since the conditions of climate and soil in Afghanistan—as in Abyssinia—are so various. Nevertheless, it is very striking that different centres should have been found for the 14, 28 and 42 chromosome forms, and there seems to me no doubt that the broad features of Vavilov's conclusions must be accepted.

In connection with these results we must again mention the problem of how to recognise the group to which a given form belongs. Although it is difficult to say on what basis all second group forms can be separated from all third group forms, if we collect from only a single country the difficulty no longer exists. Indeed it is very general in Systematics that two related species are quite distinct in any given area, but are not

easily separated if they are collected over their whole range. This is evidently to be expected. In Spain *T. vulgare* is not very diverse, and is easily distinguished from *durum*, of which a number of forms are found there, by characters that are not typical of it in other parts of its range. In Persia, again, *vulgare* is very diverse but *durum* is rare, and is separated from the former by features it lacks there but possesses elsewhere. Difficulty would evidently have occurred only if the centres of origin of the two groups had happened to coincide. It must be noted that any species to which this explanation is applied must be assumed to have arisen as an independent species—by "species mutation"—an explanation that is perhaps valid for all polyploid series.

Winge's well-known theory (1917) of the origin of polyploid series is that hybridisation between two species is followed by doubling of the chromosome number[1]. Species A with $2a$ chromosomes crossed by B with $2b$ chromosomes gives a hybrid, which may be nearly sterile, with $a + b$ chromosomes; and this by doubling of chromosome number gives a new species C with $2c = 2(a + b)$ chromosomes. The number of cases in which this theory has been experimentally confirmed is rapidly growing. *Primula floribunda* $(2x = 18) \times$ *P. verticillata* $(2x = 18)$ gives a sterile diploid hybrid $(2x = 18)$ which occasionally gives the fertile tetraploid hybrid *P. Kewensis* (somatic number $= 36$) as a bud sport—chromosome doubling having occurred somatically (Newton and Pellew, 1926). This tetraploid *Kewensis* has the appearance of a new species quite distinct from either parents.

From the almost sterile hybrid *Raphanus sativus* $\times$ *Brassica oleracea* (both with $2x = 18$) Karpechenko (1927) obtained seeds which produced fertile tetraploids with 36 somatic chromosomes, as well as some plants with from 51 to 53 chromosomes. He showed that these came from the union of polyploid gametes formed by the F_1 hybrid, which as a result of various irregularities in the reduction divisions, or occasionally earlier, produces gametes with varying chromosome numbers; 9 being most frequent but 18, 36, and intermediate numbers also occurring.

The 72 (somatic) chromosome hybrid from *Nicotiana glutinosa* $(2x = 24) \times$ *N. tabacum* $(2x = 48)$, found by Clausen and Goodspeed (1925), probably arose, as Karpechenko points out, in similar fashion to the polyploid *Raphanus* $\times$ *Brassica* hybrids. And the same is probably true for the fertile 56 chromosome hybrids, *Aegilotricum*, from *Aegilops ovata* $\times$ *Triticum dicoccoides* and *A. ovata* $\times$ *T. durum* (Tschermak and

[1] The theory was first put on a proper basis by Rosenberg's well-known work on the semi-heterotypic division.

Bleier, 1926); but here no investigation was made earlier than F_5 and F_6. Reference should also be made to *Rosa* (Blackburn and Harrison, 1924) and to *Digitalis* (Buxton and Newton, 1928).

In view of its experimental verification it must be admitted that Winge's theory gives a very probable explanation of the origin of polyploid series in nature. In principle, it clearly agrees with Percival's theory that *T. vulgare* arose as a hybrid between *Aegilops* and one of the Emmer wheats; and on the evidence given a hybrid origin might equally well be granted for the 28 chromosome species, which are much more variable than the 14 chromosome species and are distinguished by many new characters. The two theories have been kept in view in what follows.

II. GENETICS AND CYTOLOGY.

(1) Introduction.

Except in the case of the first group with the other two, all wheats can be crossed easily, giving fertile hybrids if they are of the same chromosome number, and a partially sterile hybrid if they differ in this respect.

Classic examples of Mendelian inheritance have been worked out in the genus. Thus Biffen (1905) showed that differences such as rough and smooth chaff, bearded and beardless ears, red and white chaff, are due to single factors, and later (1907) that susceptibility and resistance to attacks of *Puccinia glumarum* are inherited in the same way; while the cumulative factor theory was first suggested by Nilsson-Ehle's work on the inheritance of grain colour (1909). It is remarkable that later work has discovered very few further characters whose inheritance can be worked out with accuracy.

It is, of course, only since the work of Sakamura and Kihara that progress on the genetics of crosses between the groups has been made, and the greater part of this section will deal with species hybrids in wheat, with hybrids between wheat and *Aegilops*, and with related problems such as hybrid sterility. We shall also consider Winge's theory of the origin of speltoid mutants and the various genetic questions arising therefrom.

The chromosomes of any species of *Triticum* are all similar, and there are no obvious differences between those of different species. They are also rather long, and difficult to study in somatic cells. However, if root tips are treated with chloral hydrate the chromosomes are shortened; and it is claimed that not only can different lengths be found within a single set, but that the ratio the longest bears to the shortest varies in

different species. Constrictions also appear. The possibility of comparing the chromosomes of the different species of *Triticum* and *Aegilops* is therefore indicated (Kagawa, 1927, 1929 *a*, *b*).

(2) THE CYTOLOGY OF HYBRIDS IN *TRITICUM* AND *AEGILOPS*.

(*a*) 42 × 28 *chromosome wheats.*

The first description of the cytology of crosses between wheats with different chromosome numbers was that of Kihara (1919) for hybrids between members of the second and third groups, and we will deal with these crosses first. Later workers have confirmed his results, and altogether the following crosses have been described, viz. *polonicum* × *Spelta* and *turgidum* × *compactum* (Kihara, 1919, etc.); *durum* × *vulgare* (Kihara, 1919; Sax, 1922 *a*); *polonicum* × *compactum* (Kihara, 1921); *turgidum* × *vulgare* (Watkins, 1924). The hybrids are moderately fertile.

Wheat is not very favourable for studying the heterotype prophase and no detailed description has been given for the hybrids, but at heterotype metaphase the 35 chromosomes are present as 14 bivalents and 7 univalents (Figs. 6, 7). The constituents of the bivalents separate normally, while the univalents lag behind and split longitudinally (Figs. 8, 9). The split halves travel to the poles, but sometimes arrive too late to be included within the daughter nuclei (Fig. 10). In the homotype the chromosomes, 21 or less in number, are arranged regularly on the equatorial plate (Fig. 11); but while those descended from the bivalents split longitudinally and pass to the poles in the normal way, the univalents segregate at random (Fig. 12) and may, once again, arrive at the poles too late to be included within the nuclei (Fig. 13). A tetrad is always formed (Fig. 14) (Kihara, 1919; Sax, 1922 *a*; Watkins, 1924). In both divisions loss of chromosomes occurs at random (Watkins, 1924). Trivalent chromosomes are rare in these hybrids (Kihara and Nishiyama, 1928) and pairing seems to take place very regularly in the way described, though Sax (1922 *a*) records a probable case of nine univalents being seen, thus indicating that two chromosomes which normally pair had failed to do so. The lost chromosomes are seen in the tetrad cells as deeply staining spherical masses or as small nuclei. As the pollen grain develops they probably degenerate (Kihara, 1919; Watkins, 1924). Owing to random segregation of the 7 univalent chromosomes at the homotype the tetrad nuclei may contain any number of chromosomes from 14 to 21, and roughly 75 per cent. of these tetrads develop into

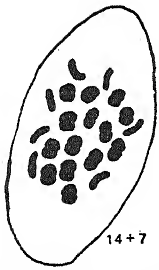


Fig. 6. Heterotype metaphase, polar view.

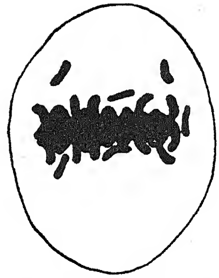
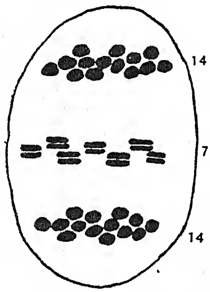
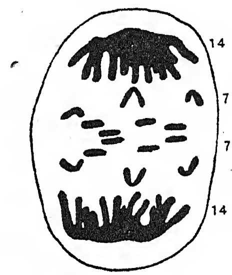


Fig. 7. Same in side view.





Figs. 8, 9. Anaphase.

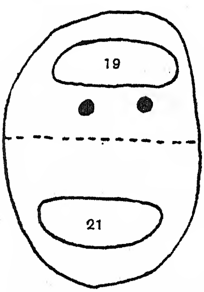


Fig. 10. Telophase.

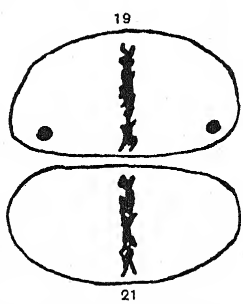


Fig. 11. Homotype metaphase.

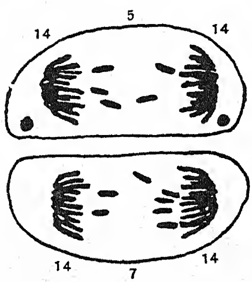


Fig. 12. Late anaphase.

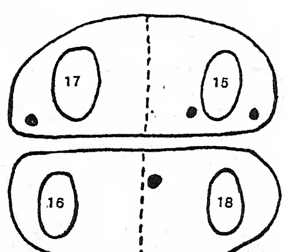


Fig. 13. Telophase.

Figs. 6–14. Reduction divisions in pentaploid wheat hybrids. Somewhat diagrammatic.

pollen grains in normal fashion. The others cease development at any time from the single nucleus stage onwards, and give at anthesis pollen grains which are completely or partially empty (Watkins, 1927*a*).

In the embryo-sac mother cell the divisions follow the same course. But in pollen mother cells univalents lost at the heterotype are often regained during the homotype, while in the embryo-sac mother cell this does not occur; so that from this cause the egg cells would have rather lower chromosome numbers than the pollen grains. Only the innermost megaspore functions (Watkins, 1925).

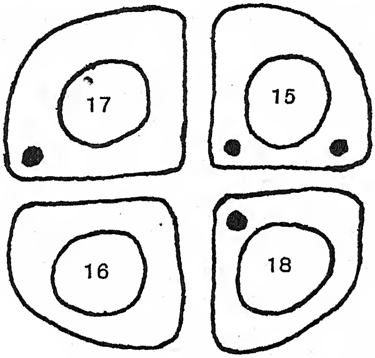


Fig. 14. Tetrad.

It is assumed that the 14 Emmer group chromosomes pair with 14 from *vulgare*, and that 7 specific *vulgare* chromosomes are left unpaired. This is the simplest supposition and appears usually to be true, but possibilities that might arise from other modes of pairing will also be considered on later pages. In any case it is clear that in F_2 we ought to find plants with any number of chromosomes from 28 to 42.

Further discussion of these crosses will be deferred until the cytology of other species hybrids has been described.

(*b*) 28 × 14 *chromosome wheats.*

Here the 21 chromosomes of the F_1 behave less regularly than those described above. The number of bivalents formed is variable and usually less than 7, while trivalents may also occur. Apparently the univalents may divide either at heterotype or at homotype. The hybrids are almost sterile.

In *dicoccum* × *monococcum* and in *aegilopoides* × *dicoccum* (Kihara, 1924) the divisions differ from the pentaploid hybrid in that the bivalents are variable in number, from 4 to 7, and their components more loosely

united. They behave regularly; but the univalents, in number from 13 to 7, may divide at either division. Later (Kihara and Nishiyama, 1928) it was reported that from 0–3 trivalents, with varying numbers of bivalents and univalents, might be found. The figures given are convincing and will be discussed later (pp. 205–6). For *turgidum* × *monococcum* Sax (1922 *a*) and Thompson (1926) give somewhat different descriptions, possibly because they used different varieties. Sax described approximately 7 bivalents and 7 univalents, but as many as 9 or 11 univalents were also observed. so that presumably only 6 or 5 bivalents might be formed. Thompson found any number from 3 to 7, usually 5 or 6, with loose association between members of a pair. According to Sax the univalents are grouped at the poles at heterotype metaphase, are joined there by the descendants of the bivalents, and divide longitudinally in the homotype. On the other hand, Thompson found that they split longitudinally in the heterotype and segregated at random in the homotype, loss being frequent.

The two series of crosses so far described, viz. 42 chromosomes × 28 and 28 × 14, are sufficient to give an idea of the general behaviour, and most of the remaining cases will be dealt with more briefly.

(*c*) 42 × 14 *chromosome wheats.*

The hybrids are sterile (Percival, 1921) or weakly fertile (Kihara and Nishiyama, 1928).

For *Spelta* × *monococcum* Melburn and Thompson (1927) give 0–5 bivalents, pairing being loose, and 28 to 18 univalents. For *Spelta* × *aegilopoides* Kihara and Nishiyama (1928) found on one occasion as many as 10 bivalents, plus 8 univalents; but 7 bivalents were more usual, and 1–2 trivalents with various numbers of bivalents—usually 4 or 5—were also found.

(*d*) *Aegilops* × *Triticum.*

A. cylindrica Host. and *A. ovata* L. have been crossed with most wheat species and the cytology described. The hybrids are sterile, and the pollen obviously imperfect with very few exceptions.

The only cases in which there is regular pairing at the heterotype are in *A. cylindrica* ($x = 14$) × *T. vulgare* described by Sax and Sax (1924), and in considerable detail by Kagawa (1928), and in *A. cylindrica* × *T. Spelta* (Bleier, 1928). In both these crosses there are usually 7 bivalents and 21 univalents, but occasionally the bivalents only number 5 or 6. In marked contrast, *A. cylindrica* ($x = 14$) × *T. durum*

($x = 14$) gives no bivalents (Bleier, 1928), obviously suggesting that *vulgare* is differentiated from *durum* by 7 chromosomes that are similar to 7 of the chromosomes of *A. cylindrica*. On the other hand, in *A. ovata* ($x = 14$) × *T. vulgare* there are either no bivalents (Percival, 1926) or there is occasional loose pairing (Bleier, 1928), so that there should be considerable differences between the chromosomes of *A. ovata* and those of *A. cylindrica*. Though no cytological study has been made, so far as I am aware, it is interesting to know (Percival, 1928) that the hybrid between the latter two species is sterile.

A. ovata ($x = 14$) × *T. monococcum* ($x = 7$) often gives 21 univalents, but sometimes up to 5 bivalents (Bleier, 1928).

In *A. ovata* × *T. dicoccum* (Percival, 1926; Sax, 1928) × *dicoccoides* (Bleier, 1928) × *durum* (Bleier, 1928), or × *polonicum* (Kagawa, 1929 *c*) pairing is absent or only loose. Bleier was unable to find evidence for the production of 28 chromosome gametes in his hybrids. They are to be expected because it was from the same cross that the fertile 56 chromosome hybrids were obtained, and the irregularities described by Percival and by Sax suggest that they are sometimes formed. Sax definitely showed their production on the female side, where however the divisions may possibly be somewhat different. He crossed his F_1 back to *dicoccum*, and out of six offspring examined all had 42 chromosomes, so that the F_1 egg cells must have had 28. The plants so obtained are interesting since they have the same chromosome number as *T. vulgare*, and are described as being like that species in many respects; but they are of course sterile, and give at reduction 14 bivalents plus 14 univalents, as indeed is to be expected from their origin.

In *A. cylindrica* × *T. dicoccum* (Kagawa, 1929 *c*) no bivalents were observed, and the formation of diploid pollen grains was to be expected from the chromosome behaviour.

Bleier (1928) also crossed his fertile *Aegilotricum* back to *A. ovata*. *A. ovata* × fertile F_1 (*A. ovata* × *T. durum*) gave as expected 14 bivalents and 14 univalents; but, very surprisingly, in *A. ovata* × fertile F_1 (*A. ovata* × *T. dicoccum*) no pairing at all was seen—an unexpected result that should be fully investigated.

(*e*) *The origin of the bivalents.*

The occurrence of trivalents in certain crosses and of 10 bivalents in *Spelta* × *aegilopoides* (Kihara and Nishiyama, 1928) is important, since it shows that autosyndesis—pairing of the chromosomes from one parent among themselves—can occur in the polyploid wheats. It should be

added that, although it is often difficult in wheat to tell whether a given structure is a bivalent or a trivalent chromosome, the figures given by these authors seem to me particularly convincing (Fig. 15). In pentaploid wheat hybrids trivalents are rare, and genetic evidence (see p. 235) shows that allosyndesis—pairing of chromosomes from different parents, in the usual manner—is the rule. Again, in *A. ovata* × *T. vulgare* and *A. cylindrica* × *T. durum* there is practically no pairing, so that the 6–7 bivalents found in *A. cylindrica* × *T. vulgare* presumably come from allosyndesis. An interesting case is the haploid *T. vulgare* (Gaines and Aase, 1926). This plant, which came from an attempt to cross *T. vulgare* with *Aegilops*, was exactly like the parent *vulgare*, except for its total sterility and profuse tillering, and at reduction gave 21 univalents, no pairing at all being reported. It is possible that this should be regarded

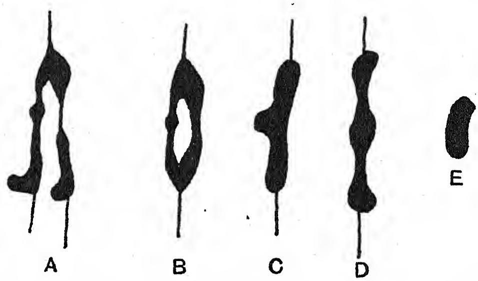


Fig. 15. Chromosomes at heterotype metaphase, in side view. A, trivalent; B–D, bivalents; E, univalent. After Kihara and Nishiyama.

as a special case, and should not be used as evidence for the amount of pairing that may occur in hybrids; but bivalents have been observed by Jorgensen in haploid *Solanum nigrum* (1928). We may probably accept the conclusion that the regular pairing found in crosses such as those just mentioned is the result of allosyndesis; but that autosyndesis is a likely explanation of the occasional pairing found in *A. ovata* × the tetraploid wheats, and probably in other similar cases, as Percival suggested (1926).

The usual practice, with which most will agree, is to regard the haploid chromosome complements of the different *Triticum* and *Aegilops* species as made up of 1, 2, 3 or more sets of 7 chromosomes; and in this way Gaines and Aase (1926) suggest that, to agree with the observations on chromosome pairing, *T. turgidum* should be represented as *ab*, *T. vulgare* as *abc*, and *A. cylindrica* as *cd*. It will be noticed that the results agree with Percival's views on the relation between wheat and *Aegilops*, inasmuch as *A. cylindrica* seems to have some relation with

T. vulgare but none with the 28 chromosome wheats. They are, however, not in accordance with the idea of a close relationship between *T. vulgare* and *A. ovata*.

No doubt the cytology of *Aegilops* and *Triticum* hybrids will help us to understand evolution in these genera, but before conclusions are drawn it should be worked out more thoroughly than it has been so far. It is also possible that the formation of bivalents gives only a rough guide to the relation between the species that enter a cross. Thus *Primula verticillata* and *P. floribunda* appear to be well separated species and give a completely sterile hybrid; but in the latter 9 bivalents are formed and the divisions are quite regular (Newton and Pellew, 1929); and Bleier's conclusions, given above, also suggest the possibility that complications may exist.

(3) CHROMOSOME BEHAVIOUR AND STERILITY IN PENTAPLOID WHEAT HYBRIDS.

(a) *General features.*

Different workers have come to different conclusions as to the cause of sterility in these hybrids, and in the following discussion I shall give as far as possible the evidence for the different views, although on some points it is not possible to come to a definite decision. I have already described the chromosome behaviour in the F_1 from crosses between the two groups, and I shall here make the simplest assumptions there suggested, viz. that the unpaired chromosomes come from *vulgare*, that the same ones always remain unpaired, and that they differ in definite ways from the others.

In any cross between the two groups the F_1 has a moderate proportion of its pollen obviously imperfect—usually about 25 per cent.—and fails to set grain in many flowers. The grains obtained may be plump and well filled, or wrinkled in greater or less degree; they germinate badly, and many of the F_2 plants die young or cease development before grain is set. Again, the F_2 plants vary greatly in the proportion of imperfect pollen and show every gradation from setting no grain to setting grain perfectly; while further, if any plant shows sterility in these features some of its progeny will die in the young stages. We may therefore recognise four aspects of sterility: imperfect pollen; failure to set grain; bad germination of grain; and non-viable zygotes. Confusion is sometimes caused by using the term sterility for any or all of these without specifying which; though, of course, all are usually associated.

Imperfect grain setting is most easily seen, and it is agreed (*e.g.* Kihara, 1921, 1924; Sax, 1922 *a*; Watkins, 1924, 1925) that this is characteristic of all plants with chromosome number intermediate between 28 and 42. Though it has been reported (Kihara, 1924) for a 28 chromosome plant it is not so usual. Closely connected with sterility are problems raised by the chromosome number and composition of the plants belonging to F_2 or later generations, and this will be described first.

We have seen that both microspores and megaspores should have any number of chromosomes from 14 to 21, and it has been abundantly confirmed (Kihara, 1919, 1921, 1924; Sax, 1923; Watkins, 1924) that, as we should expect, F_2 plants have any number of chromosomes from 28 to 42. Among these plants we can distinguish certain main ways in which the chromosomes are combined (Kihara, 1921, 1924; Watkins, 1924). Thus plants with 35 chromosomes, or less, show normally 14 bivalents + 0...7 univalents, and such plants are of normal vigour and more or less fertile. On the other hand, in plants with more than 35 chromosomes the sum of the bivalents and univalents is nearly always 21 (*e.g.* 16 bivalents + 5 univalents, 19 bivalents + 2 univalents, etc.), and such combinations are again more or less fertile and vigorous. These two types are called by Kihara fertile combinations. Occasionally, plants with other combinations are found (*e.g.* 15 bivalents + 4 univalents, or 20 bivalents only, etc.). These plants are dwarf and sterile, or nearly so, and are called by Kihara sterile combinations. That is to say that, in general, unless one complete set of 7 extra chromosomes is present none of the extra chromosomes will be present as bivalents. The exceptions are the rare so-called sterile combinations.

The explanation of this has been studied closely by Kihara (1921, 1924) and myself (1924, 1925, 1927). Kihara assumed (1924) that the 7 unpaired chromosomes of the F_1 were all different—$A, B, C, \ldots G$—and that only like chromosomes would pair in the zygotes. My own assumption was the same (1924). For simplicity we will illustrate the conclusions by supposing that instead of an F_1 with 14 bivalents + 7 univalents we have one with x bivalents + 2 univalents, A and B, genetically different. The parents would be $2x$ and $2(x + A + B)$ and the F_1 gametes of four kinds, viz.:

$$\begin{array}{llll} ♀\, x, & x + A, & x + B, & x + A + B, \\ ♂\, x, & x + A, & x + B, & x + A + B. \end{array}$$

Random mating would give the following zygotes:

No. of chromosomes	Composition	Chromosomes at heterotype
$2x$	$2x$	x biv.
$2x+1$	$2x+A$ or $2x+B$	x biv. $+1$ univ.
$2x+2$	$2x+2A$ or $2x+2B$	$(x+1)$ biv. (=sterile combination)
	or $2x+A+B$	x biv. $+2$ univ.
$2x+3$	$2x+2A+B$ or $2x+A+2B$	$(x+1)$ biv. $+1$ univ.
$2x+4$	$2x+2A+2B$	$(x+2)$ biv.

In this illustration the only sterile combination is $(x + 1)$ bivalents, $2x + 2A$ or $2x + 2B$; and this is a sterile combination because an extra chromosome is present as a bivalent without a complete set of the extra chromosomes—here a complete set is $A + B$—being present. The case of 7 univalents is of course far more complicated and the sterile combinations are far more numerous. Examples of the combinations when there are 7 univalents are:

$$\text{Fertile combinations} \begin{cases} 2X + A + B, \quad 2X + B + C + E + F + G, \\ 2X + 2A + 2C + B + D + E + F + G, \end{cases}$$

$$\text{Sterile combinations} \begin{cases} 2X + 2B, \quad 2X + 2C + D + F + G, \\ 2X + 2A + 2B + 2C + 2D + 2E + F, \end{cases}$$

where $2X$ represents the 14 bivalents and $A, B, \ldots G$ the 7 univalents. The frequency of the various possible combinations has been worked out in detail by Kihara (1924), assuming random segregation of univalents at the homotype and no chromosome loss, and by myself (1924) assuming random segregation and allowing for chromosome loss. Roughly speaking, from 10 to 90 per cent. of the combinations would be expected to be sterile combinations, according to the chromosome number of the parent plant, the maximum occurring for 36 chromosome plants.

The actual rarity of these sterile combinations is an important fact. Closely related to it is another, equally important and verified experimentally by many counts (Kihara, 1924), namely that plants with less than 35 chromosomes, the "Verminderungsgruppe" of Kihara, give progeny with the same number or fewer, so that by continued self-fertilisation the number 28 is finally reached. On the other hand, plants with more than 35, called by Kihara "Vermehrungsgruppe," give with few exceptions progeny with an equal or greater number of chromosomes, so that finally the number 42 will be reached. This is, in fact, a direct consequence of the absence of the sterile combinations, as shown by Kihara (1924) and by myself (1924). In the case of a 40 chromosome plant, for example, all offspring with fewer than 40 would have less than a total number of 21 (bivalents + univalents) and would be sterile combinations (Diagram 1 *a*, *b*).

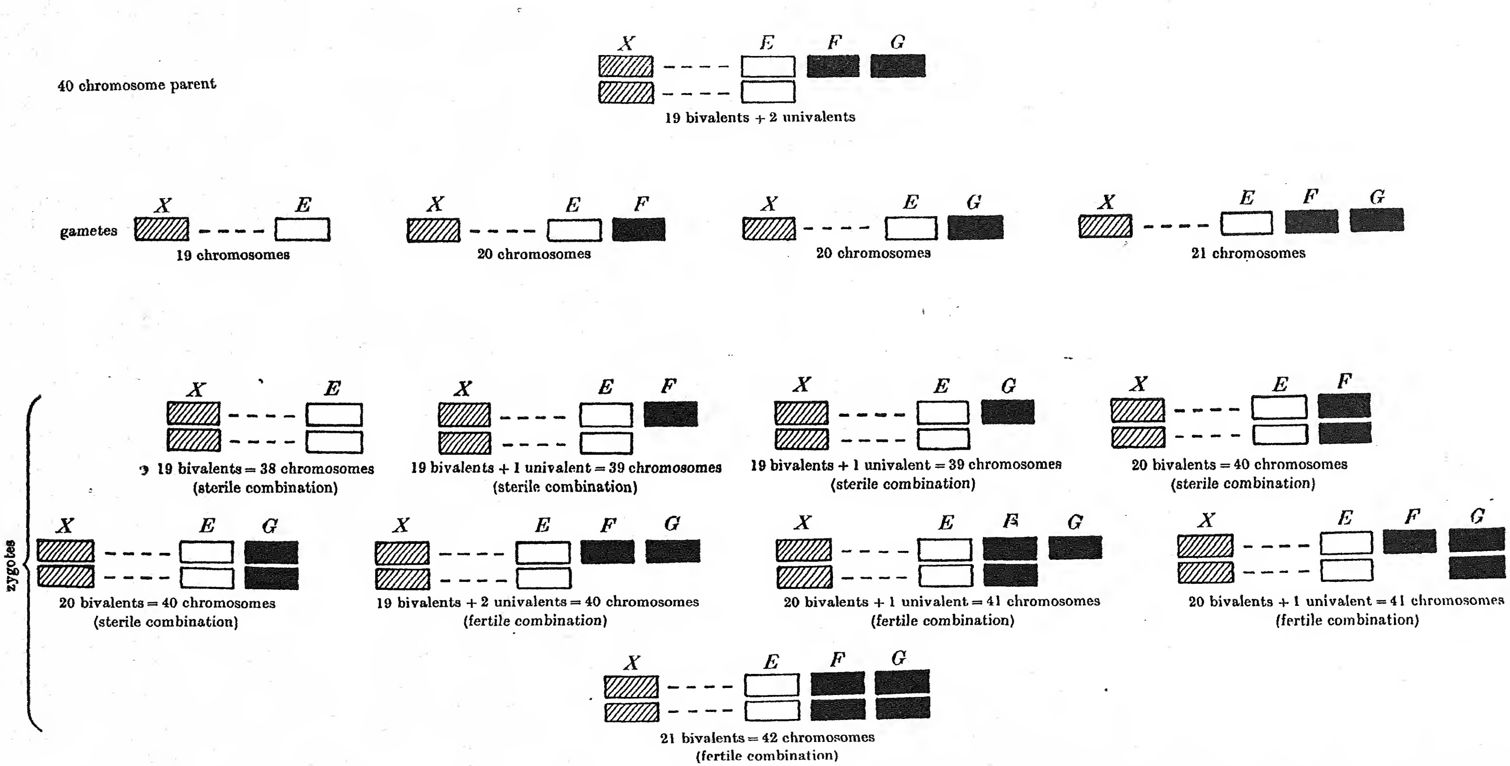


Diagram 1 *a.* Offspring of a 40 chromosome plant; showing that all plants with less than 40 chromosomes will be sterile combinations. The plant originated from a cross between a tetraploid wheat with $2X$ chromosomes and a hexaploid with $2X+2(A+B+C+D+E+F+G)$ chromosomes.

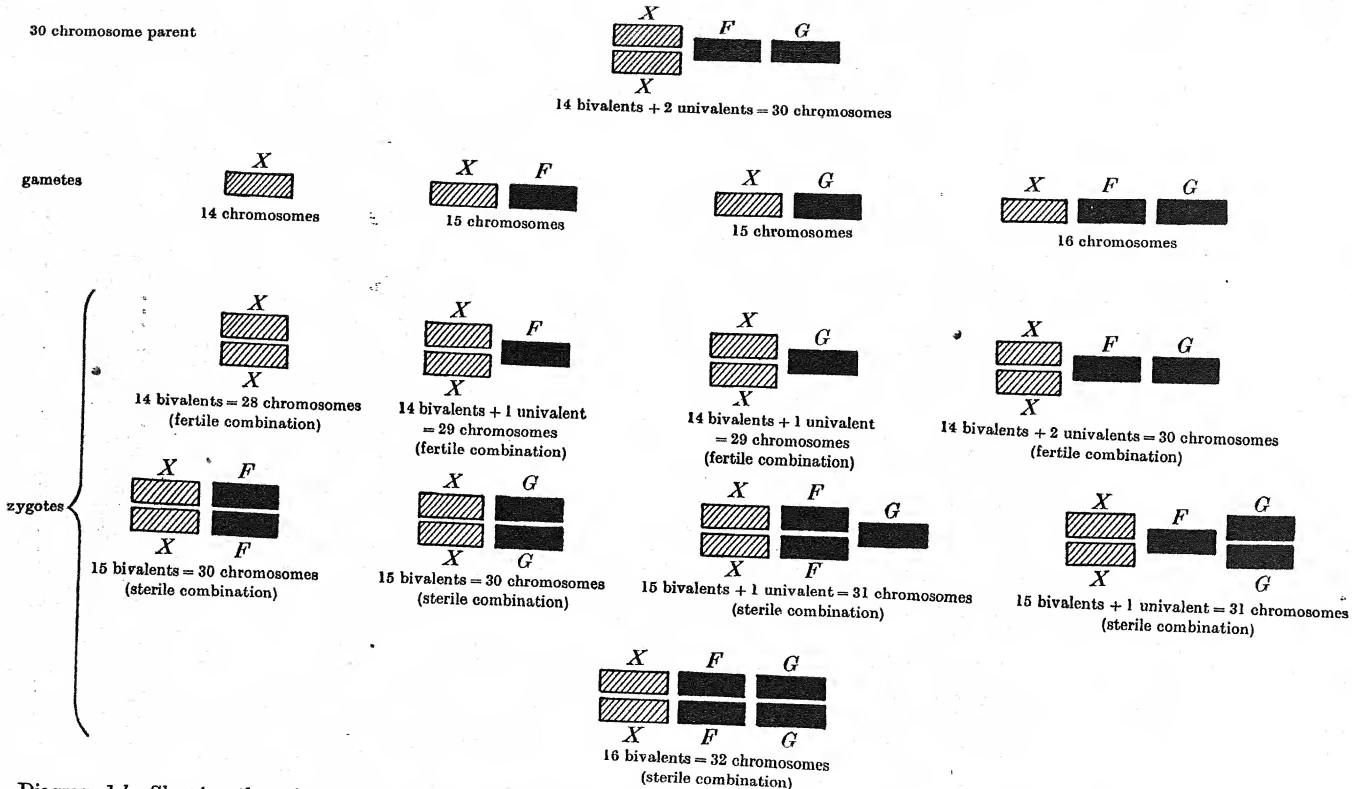


Diagram 1 *b*. Showing that the offspring of a plant with 30 chromosomes will be sterile combinations if their chromosome number is more than 30. $X = 14$ chromosomes derived from Emmer or *vulgare*. The 30 chromosome plant was derived from the cross Emmer with X chromosomes $\times$ *vulgare* with $(X+A+B+C+D+E+F+G)$ chromosomes.

From what has been said it is evident that a true breeding segregate with chromosome number intermediate between 28 and 42 would be exceptional.

These facts are important to understand, both for the genetics of the cross and for the problem of sterility, but before dealing with these questions some results described by A. A. Sapehin (1928) and by A. A. and L. A. Sapehin (1928) must be mentioned.

These results refer to cytological irregularities observed within the species *vulgare* and in a *durum* × *vulgare* cross. Two types of irregularity were described. In one of these the heterotype division is disorderly, the chromosomes vacuolise, and dyads or tetrads with many nuclei, apparently degenerating, are formed. This was observed in some varieties of *vulgare* and is clearly a physiological question outside the scope of this paper. In the other type irregular production of univalents was observed. Thus, varying numbers of univalents were found in pure lines of *vulgare* and in true breeding F_1 extracts from *durum* × *vulgare*, with 42 chromosomes. In some lines this was observed only in a few tenths per cent. of cases (? cells); but occasionally in as many as 3–4 per cent. of cases; while in an F_2 from two such lines the frequency varied from 0 to 60 per cent. Another case was a 36 chromosome plant "showing...a fair fertility," which bred true to chromosome number and type. The plant had 16 bivalents + 4 univalents, and until it has been ascertained how such a combination of chromosomes can breed true to chromosome number its significance cannot be discussed. The final case refers to a 36 chromosome plant with 5 bivalents + 14 univalents, a total of 24 chromosomes; but this does not seem to be quite clear.

The meaning of these results evidently cannot be discussed until they have been more fully worked out.

(*b*) *Sterility: Introductory.*

In this section the conclusions of the different workers will be briefly described.

Kihara's work on sterility has been directed towards explaining the absence of the sterile combinations of chromosomes. Assuming no loss of univalents at reduction, and random mating between the gametes, he worked out the frequency of the various possible chromosome numbers among the offspring of 36, 37, ... 41 chromosome plants. Comparing this expectation with the frequency found experimentally he concluded that these assumptions were correct, and that zygotes with sterile combinations were formed but were afterwards eliminated in

various ways. The conclusion was confirmed by observations on the number of flowers per ear that set grain, the number of grains that germinated, and so on.

Sax (1922 *a*) measured sterility in F_1 and F_2 by average number of grains per spikelet, and also in F_1 observed the proportion of visibly bad pollen. Assuming that grains did not set when the egg cells were not functional, he concluded that both male and female gametes with chromosome numbers intermediate between 14 and 21 tended to be eliminated, those with 17 and 18 chromosomes being most affected. Other factors, such as poor vegetative development, and qualitative differences between the homologous chromosomes of the parent species, were also thought to operate. Later (1928), he concluded from reciprocal crosses between an F_1 and its parents that "loss of univalents, selective elimination of gametes, and possibly selective fertilisation, do not seem to be adequate to account for the great excess of 14 chromosome gametes."

My own work has been partly directed to explaining the absence of the sterile combinations. It was found that univalents were lost at random at reduction, and by observing the amount of loss the frequency of the different chromosome numbers in the gametes was calculated. In some cases random mating gave a high proportion of sterile combinations (about 90 per cent. of the offspring of a 38 chromosome plant, and about 25 per cent. of a 31 chromosome) which could not be accounted for by the observed amount of zygotic mortality. Hence, since nearly all F_1 egg cells were shown to be fertile with parental pollen, it was concluded that there had been elimination of pollen with intermediate chromosome numbers, which would of course greatly reduce the proportion of sterile combinations. This was confirmed by the low pollen germination observed on the F_1 stigmas; and by a small number of chromosome counts for reciprocal crosses between F_1 and the parents.

Thompson and Hollingshead (1927), calculating the frequency of chromosome numbers in F_1 gametes on the basis of random segregation of univalents in the homotype, found that in F_2 from *dicoccum* × *vulgare* the proportion of 28 chromosome plants was actually far higher than was expected. They considered that this was to be accounted for partly by loss of univalents at reduction in the F_1, partly by bad grain germination, and partly by sterility in the gametes. Later (1928) Thompson and Cameron made reciprocal crosses between various F_1's and their parents; and, comparing the results with expectation, concluded that there was elimination of gametes with intermediate chromosome numbers in both male and female, but chiefly in the former.

Evidently there is much disagreement among the different workers, and it will therefore be necessary in the following pages to discuss each aspect of sterility in some detail. Even so, though on some points we can reach definite conclusions, on others this will not be possible. To some extent different workers have used different crosses, but it seems to me unlikely that there will be any important differences in principle between them, though we should of course expect considerable variation in the intensity with which the various factors operate.

(*c*) *Grain germination.*

I shall consider this first since the conclusions seem reasonably certain; namely, that germination depends upon whether there are one, two, or three sets of the extra chromosomes of the *vulgare* group present in the endosperm (Watkins, 1927 *a*).

Sax (1922 *b*) pointed out that, in wheat, sterile crosses give wrinkled F_1 endosperms, and suggested that this was associated with the parental difference in chromosome number; in F_2 he found that the endosperms were variable, and unrelated to the sterility of the plant their embryos produced (1922 *b*). Kihara (1924) considered the possibility that some of the embryos with sterile combinations might be eliminated by bad grain germination, but though this may be an added cause there seems little doubt from my own work (1927 *a*) that the endosperm is the most important factor. In the normal endosperm all chromosomes are triploid, two sets being derived from the polar nuclei and one from the male gamete; so that *vulgare* endosperms will have 63 chromosomes, and those of the Emmer wheats 42. Reciprocal crosses between 28 and 42 chromosome plants will give different endosperms: ♀ 28 chromosome × ♂ 42 giving one with $14 + 14 + 21 = 49$ chromosomes, and ♀ 42 × ♂ 28 one with $21 + 21 + 14 = 56$. It is found that in the former cross the grains obtained are wrinkled and germinate badly, while in the latter they are not wrinkled, though below normal size, and germinate well. In these crosses, as in all others investigated, the classes that germinate badly have the extra *vulgare* chromosomes haploid in the endosperm while those that germinate well have them diploid. The clearest confirmation is given by reciprocal crosses between F_1 and the 28 chromosome parent. F_1 pollen has any number of chromosomes from 14 to 21, and the cross ♀ 28 chromosome × ♂ F_1 gives two classes of grains, viz. unwrinkled grains that germinate well and produce 28 chromosome plants, and wrinkled grains that germinate badly and give plants with more than 28 chromosomes, chiefly from 31 to 35. Evidently the extra

chromosomes, which are present once each in the endosperm, as well as in the embryo, are the cause. But in the reciprocal cross, ♀ F_1 × ♂ 28 chromosome, although many of the embryos have extra chromosomes as before, the endosperm in such cases will have them present twice each instead of once; and it is therefore found that the grains are not wrinkled and germinate well. Reciprocal crosses between F_1 and the 42 chromosome parent also agree with these results, so it was definitely concluded that in pentaploid wheat hybrids the grains germinate badly if the extra chromosomes are haploid in the endosperm, and well if they are diploid or triploid. It was not found whether there is any difference in the germination in the last two classes, but as noted above they are sometimes different in appearance.

The results given refer only to crosses between *vulgare* and *turgidum*, but it may be stated here that they have been amply confirmed for a number of other crosses between the two wheat groups (unpublished), and it is of course probable that the conclusions will apply to the polyploid series in other genera, and may often be the reason for the shrivelled seeds that are so typical of many hybrids.

It should be pointed out, however, that although the factor in question must be the usual cause of the poor germination of grains of F_2 or later generations in wheat hybrids—which is indeed confirmed by the shrivelled appearance of many of them—there still remains the possibility, as yet unproved, that the constitution of the embryo may also operate.

(*d*) *Failure to set grain.*

Writers on sterility often refer to this feature alone when the term sterility is used, probably because it is the most obvious and easily measured; but the practice is sometimes confusing, and it would be better when speaking of sterility to specify exactly which form is meant.

Kihara (1921, 1924), Sax (1922 *a*) and I (1925) have all come to different conclusions. I will give my own results first as they seem to me conclusive so far as they go, and the only question is how widely they may be applied.

Crosses between different species give F_1's with different amounts of fertility. Under Cambridge conditions most set grain in about 75 per cent. of flowers, but in *Spelta* × *persicum* the fertility is much lower. In F_2 and F_3 it varies from 0 to 100 per cent. Perfect success in crossing wheat is not easily attained, but crossing F_1 (*vulgare* × *turgidum*) back to its parents (1925) gave a success of $136/157 = 87$ per cent., while crosses

between pure lines gave 90 per cent., and the F_1 allowed to self set 75 per cent. It seems conclusive that in this F_1 some of the F_1 egg cells, though functional, fail to become fertilised by their own pollen—it was in fact observed that pollen germination was often low on F_1 stigmas—and if any egg cells are non-functional the proportion must be less than 5 per cent. (1925). The result has been repeated for several years for this F_1, and has been found to apply also to a number of other crosses, *e.g. vulgare* × *dicoccum*. Since this is evidently a frequent cause for failure to set grain in F_1, I think it may be extended to some, at any rate, of the F_2 and F_3 plants. Moreover, cytological observation showed (1925) that in several F_3 plants which only set grain in about 50 per cent. of flowers there were only 8 per cent. of aborted embryo sacs, while 43 per cent. of those that were morphologically perfect failed to become fertilised. It is still possible that in some plants, especially the most sterile, other factors may operate; but evidently the one in question is important and it has been entirely neglected by other workers.

In *durum* × *vulgare* and *turgidum* × *compactum*, Sax (1922 *a*), measuring sterility by number of grains per spikelet, assumed it was due to non-functional egg cells alone, and suggested that it was chiefly those with 17 and 18 chromosomes that did not function. No direct evidence was put forward in support, and it is clear from what has been said above that this view must be largely wrong. But on general grounds it is quite likely that in the more sterile plants some of the egg cells are actually non-functional, and the 8 per cent. found above may be an example. But as yet we have no evidence as to the exact cause.

Kihara (1924) considered that in flowers that did not give grain the embryo had aborted, and that the sterile combinations of chromosomes were eliminated thereby. "Nachdem die Embryonen durch Verschmelzung von verschiedenen chromosomigen Gameten gebildet sind, werden dieselben in ihren verschiedenen Entwicklungstadien eliminiert. Daher sind die Körner einer Ähre, die gut entwickelt sind, grössenteils solche, die als Embryonen von fertilen Kombinationen zu erklären sind." Following this idea he worked out the relative frequency of zygotes with sterile and fertile combinations to be expected from the self-fertilisation of plants with 35, 36, ... 41 chromosomes; assuming that no chromosomes were lost at reduction, that univalents segregated at random during the homotype, and that there was random mating between the gametes so formed. For example, a 40 chromosome plant would give 9 zygotes with fertile combinations to 7 with sterile. It was then sug-

gested that if a completely fertile (42 chromosome) plant set 30 grains per ear the 40 chromosome one would set $9/16 \times 30 = 16{\cdot}8$ grains per ear. In this way he worked out the variation in fertility with change of chromosome number from 35 to 42; and comparing the results with the observations for a number of plants of known chromosome number it was considered that the agreement was sufficient to support the theory. Since, however, the two assumptions—random mating (see below, p. 218) and no loss of univalents—are neither of them correct, the calculations can only have comparative value. It should also be pointed out that number of grains per ear is not a reliable measure of the proportion set, which is what is wanted, since it varies greatly with the vigour of the plant. Kihara also found that in a 39 chromosome plant, for example, the observed frequency of offspring with 39, 40, 41, 42 chromosomes agreed with the calculations given above if only the fertile combinations survived and zygotes with sterile combinations were eliminated. But agreement was good only for the progeny of 38 and 39 chromosome plants. In the case of 40 and 41 chromosome plants it was not good, and the reason suggested was loss of chromosomes in the reduction divisions—a possibility that was not considered in the former case. Against Kihara's conclusion that failure to set grain is caused by the abortion of embryos with sterile combinations of chromosomes is the positive evidence that, in a number of partially sterile plants from *vulgare* × *turgidum* (Watkins, 1925), cytological examination showed that in those flowers in which no grain was set the egg cells were not fertilised, and that, with one or two doubtful exceptions out of over 70, fertilised egg cells developed normally and gave normal grain. Hence, it seems to me certain that the mechanism suggested by Kihara cannot be a widely spread cause of sterility.

Finally, my own conclusion has been criticised by Thompson and Cameron (1928), working with *vulgare* × *durum*, × *dicoccum*, and × *dicoccoides*; first on the ground that, when F_1 was crossed back to the parents, chromosome counts showed that some of the egg cells with intermediate numbers had been eliminated; secondly, because less seed was obtained when F_1 was pollinated from the parents than in crosses between pure lines. The first of these criticisms does not seem to me valid for reasons given below (p. 221). With regard to the second, some reason connected with the technique of making the crosses seems to be indicated, since a set of only 34 per cent. was obtained, and similar F_1's set 75 per cent. when allowed to self (Thompson and Hollingshead, 1927), as they do at Cambridge.

In conclusion, I think it may be said that in most crosses between the second and third groups, the reason for failure to set grain in the F_1, and often in plants of later generations, is that egg cells that are functional with parental pollen do not get fertilised by their own pollen; though the exact reason for this is obscure. It is also possible, especially in the more sterile plants, that some egg cells may be non-functional (Sax, 1922 *a*), and that in some cases there may be embryo abortion (Kihara, 1924); but neither of these suppositions has yet been proved.

(*e*) *Elimination of zygotes.*

It is probable (Kihara, 1924; Watkins, 1925) that plants which die in the young stages, or do not complete development, have sterile combinations of chromosomes; indeed this is almost certain from Kihara's work. Development may stop at almost any stage. Some die when only a few leaves have been formed, others tiller abundantly but produce no ear; some die just before or after the time of the reduction divisions, and in others the ear does not escape properly from the sheath, or emerges but is sterile. Kihara actually found a few plants with the sterile combinations of chromosomes (*e.g.* 20 bivalents, 16 bivalents + 2 univalents) and these were dwarf and sterile, or at the best only weakly developed and moderately fertile. It seems therefore reasonable to conclude that plants that die at various stages during growth are also so constituted.

We shall notice later (p. 241) other examples of the weak development of plants with sterile combinations of chromosomes.

(*f*) *Pollen sterility.*

Kihara first assumed (1921) that all pollen classes were equally functional; but though for the most part he held the same view in his later work on the evidence discussed above (p. 216), he did deal with the possibility of different pollen tube growth rates in an appendix (1924), and these results may now be given. Reciprocal crosses were made between a 41 and a 42 chromosome plant, and chromosome counts in the offspring gave the following frequencies for the functional gametes of the former:

	20 chromosomes	21 chromosomes
♀	11	4
♂	6	8

This clearly suggests that 21 chromosome pollen is favoured at the expense of that with 20, in the plant in question. It is not clear whether

this plant came from *durum* × *vulgare* or *polonicum* × *Spelta*, but it is not material.

My own work refers to *turgidum* × *vulgare*, and the question first studied (1924) was the absence of the sterile combinations of chromosomes. In a plant with 38 chromosomes (17 bivalents + 4 univalents), for example, the chromosome loss was counted, and from this were calculated the frequencies of microspores with 17, 18, ... 21 chromosomes. Had there been no loss, those with 17 and 21 chromosomes would of course be equally frequent; but actually those with 17 (20 per cent.) greatly outnumber those with 21 (about 1 per cent.); and, in consequence, random mating would give a high proportion (about 90 per cent.) of sterile combinations. In a 31 chromosome plant (14 bivalents + 3 univalents) about 43 per cent. of microspores had 14 chromosomes, only about 1 per cent. had 17; and random mating would give only about 30 per cent. of sterile combinations. The great difference in the two cases is, of course, due to the fact that chromosome loss increases the proportion of microspores with a low chromosome number and decreases those with a high number, leading thus to an increase in the number of sterile combinations from a plant with more than 35 chromosomes, and to a decrease in the number from one with less than 35. It was then found (1925) that, in several plants with more than 35 chromosomes, such a high proportion of sterile combinations was not accounted for by the observed amount of zygotic mortality; as shown by the fact that embryo abortion could not be found, by tests of grain germination, and by the number of plants that died. Hence it was concluded that there must have been elimination of pollen with intermediate chromosome numbers in favour of those with either 14 or 21, or near to these two. To confirm this it was shown that although about 80 per cent. of F_1 pollen is morphologically perfect, only about 10 per cent. germinates on the stigmas, so that considerable selective elimination is possible. Later (1927 *a*) the F_1 crossed back reciprocally to its parents with the following results:

	No. of chromosomes in functional gametes							
	14	15	16	17	18	19	20	21
F_1♂	13	3	0	3	5	2	6	4
F_1♀	2	4	2	1	1	1	0	0

These figures confirm the conclusion since the expectation for both sexes was a binomial distribution with the mode at about 16. In criticism it must be admitted that the counts are small, and that the previous conclusion rested on indirect evidence. But, on the other hand,

there is a very striking discrepancy between the small number of zygotes actually eliminated and the 90 per cent. or so of expected sterile combinations if random mating is assumed. It seems fairly certain that in these plants, with more than 35 chromosomes, there must be a favouring of 21 chromosome pollen grains at the expense of those with lower numbers. For plants with less than 35 chromosomes, where the expected proportion of sterile combinations is much smaller, the evidence is not so strong; and elimination of gametes with 15 or 16 chromosomes in favour of those with 14 may be less marked.

Further evidence is given by Nishiyama (1928) who worked with two 41 chromosome plants. These came from crosses between *T. Spelta* and two dwarf plants with 20 bivalents (a sterile combination) which were themselves obtained by Kihara (1924) from the cross *polonicum* × *Spelta*. The two plants were crossed back to both their parents. In the female the ratio of 20 : 21 chromosome gametes was 73 : 27; the departure from equality being due to chromosome loss, and being in agreement with my results given above. For the male, however, the corresponding ratios were 11 : 89 and 37 : 63 in the two plants, clearly showing elimination of 20 chromosome pollen grains. Nishiyama's paper is in Japanese and it is not clear from the English summary to what extent actual counts were made, and to what extent the number of chromosomes was estimated from the characters of the plants; but in any case the latter method should be a reliable guide in such a case.

Working with *vulgare* × *dicoccum*, × *durum*, and × *dicoccoides*, Thompson and Cameron (1928) give the results of a large number of aceto-carmine counts when F_1 was crossed back reciprocally to the parents. Different F_1's gave similar results with one exception which was probably significant, though the number of counts was not very large. The data must be discussed in detail below, but the conclusion was that there was elimination of both male and female gametes with intermediate chromosome numbers, and more in the male than in the female.

Although random mating was assumed by Kihara (1924) in most of his work, it will be noticed that he did later on consider the possibility of a selective sterility in the pollen; and later work (Nishiyama, 1928; Thompson and Cameron, 1928) supports my own conclusion (Watkins, 1925) that this does occur. Sax also (1922 *a*) had assumed that there was such a selective action, but did not give much evidence in support. We must, however, defer our conclusion until certain other evidence has been examined.

(*g*) *The functional gametes and the F_2.*

In this section we may consider in detail some data given by Thompson and Hollingshead (1927), Thompson and Cameron (1928), and by Sax (1928) which may have an important bearing on the matters we have been discussing above. The data appear to show an unexpected excess of 28 chromosome plants in F_2. There is evidence that this only occurs to a marked extent in some crosses, but we shall have to consider the possible bearing of the phenomenon on our previous conclusions in case it should occur less markedly in other cases as well.

The first instance was given by Thompson and Hollingshead (1927) in *vulgare* × *dicoccum*. Counts were made for 28 plants by the aceto-carmine method, and "an attempt was made in each case to ascertain the numbers of bivalents and univalents." Allowing for possible uncertainty in the counts it does not seem likely that a mistake could have been made with 28 chromosome plants, and yet no less than 6 of these were found among the 28 plants counted. The authors point out that random segregation of 7 univalents at the homotype means, if there is no loss, only $(\frac{1}{2})^7 = 1/128$ microspores or megaspores with 14 chromosomes; thus giving, with random mating, less than one 28 chromosome zygote per 10,000. They consider that the discrepancy may be due partly to chromosome loss at reduction, partly to mortality of zygotes, and partly perhaps to the 25 per cent. sterility of F_1 flowers, since these might represent embryos that fail to develop.

The interesting feature of the results is that all these factors together are not enough to explain the discrepancy. 25 per cent. of the flowers on the F_1 gave no grain; of the grains, 37 per cent. germinated; and it is to be presumed that the 6/28 plants with 28 chromosomes were a random selection. If we make the unlikely assumptions (1) that every 14 chromosome egg cell was fertilised (the flowers with no grains representing egg cells with more than 14 chromosomes), (2) that every one was fertilised by a 14 chromosome male gamete, and (3) what is probably nearly true, that every grain with a 28 chromosome embryo germinated, we can then find the minimum proportion of 14 chromosome egg cells the F_1 plant must have had. It comes to $6/28 \times 0{\cdot}37 \times (1{\cdot}0 - 0{\cdot}25) = 0{\cdot}06$; and this is still a high proportion. We have seen that random segregation of univalents in the homotype, with no loss, would mean a proportion of $(\frac{1}{2})^7 = 1/128$. Actually, of course, there is loss of chromosomes, and from the amount observed by the authors in the tetrads we can calculate that the true frequency of 14 chromosome microspores would be

$(0{\cdot}54)^7 = 0{\cdot}013$; while the frequency found above for megaspores, $0{\cdot}06 = (0{\cdot}67)^7$, requires a much heavier loss than was observed. Assuming the accuracy of the figures, there is an evident disagreement between observation for the egg cells and expectation from chromosome behaviour in pollen mother cells. There are two objections—the rather small number of counts, and the possibility that not all the lost univalents were still seen when the tetrads were examined—but other results to be given below lead to a similar conclusion.

Considering in more detail Thompson and Cameron's (1928) results with back-crosses referred to above (p. 220) no special comment is needed for the exceptional cross, which gave:

	No. of gametes with 14 to 21 chromosomes							
	14	15	16	17	18	19	20	21
♀	1	1	5	8	7	3	2	2
♂	3	2	0	1	2	2	0	5

and therefore confirms the conclusion already reached about pollen sterility. The remaining crosses have been grouped together and give the following results:

	Proportion of gametes with 14 to 21 chromosomes								
	14	15	16	17	18	19	20	21	No. of counts
♀	0·36	0·14	0·15	0·14	0·10	0·07	0·01	0·02	86
♂	0·40	0·20	0·10	0·07	0·03	0·02	0·06	0·11	99

They suggest a reduction in the male gametes with from 16 to 19 chromosomes in favour of those with 20 and 21; but the proportions of those with 14 and 15 do not seem to differ much from the female. The difference between the two in the case of 16 to 21 chromosome gametes may perhaps have been reduced by the poor germination of the grains obtained when F_1 is used as male parent (see above, p. 214). Thompson considers that in addition there has been an elimination of egg cells with intermediate chromosome numbers since the numbers found do not agree with expectation based on random segregation of univalents without loss. I give below the expectation on this basis, and also that if a moderate loss is assumed:

	Expected proportions							
	14	15	16	17	18	19	20	21
(*a*) $(\frac{1}{2}+\frac{1}{2})^7$ = random segregation and no loss	0·01	0·05	0·16	0·28	·028	·016	0·05	0·01
(*b*) $(0{\cdot}6+0{\cdot}4)^7$ = random segregation and moderate loss	0·03	0·12	0·26	0·29	0·20	0·08	0·01	0·002

If either of these theoretical frequencies were correct no comment would be necessary as to their difference from the counts given above;

and we might accept Thompson's conclusion that they showed elimination of female gametes with intermediate chromosome numbers. But it is quite clear that neither of them can be correct. The success in back-crossing was about 34 per cent., and most of the counts refer to crosses in which grain germination was about 77 or 90 per cent. It follows that if we take (*b*) above as our basis, and assume that only gametes with from 15 to 20 chromosomes were eliminated, the proportion of 14 chromosome egg cells found could not be more than $0{\cdot}03 \times 100/34 \times 100/77 = 0{\cdot}11$. The counts, however, showed $31/86 = 0{\cdot}36$, so that our expectation appears to be wrong. It was based on two assumptions: (1) random segregation of univalents at the homotype, and (2) a moderate chromosome loss, about the same as that observed in the male by several authors. If there were a greater loss of chromosomes in the female than in the male, we could explain the observed excess of 14 chromosome egg cells, but unfortunately it is then found that the observed number of those with 21 chromosomes is much too high. Hence we can only conclude that the univalents do not segregate quite at random—there must be a tendency, perhaps only slight, for them to go together to the same pole—and this would clearly produce the observed deficiency of female gametes with intermediate chromosome numbers. This seems to be the only explanation of Thompson's counts, and it suggests that we should examine in more detail reduction in the female, and the question of random segregation.

Random segregation has always been assumed, but is difficult to prove. The only actual observations were made on pollen mother cells in *turgidum* × *vulgare* (Watkins, 1924), where it was found that agreement with expectation was "not very close" though "on the whole favourable to the assumption that random segregation" takes place; so that direct observation clearly suggests some uncertainty. It will be recalled that reduction in the megaspore mother cells follow the same general course as in microspore mother cells, but that there was probably a greater chromosome loss from the innermost, functional, megaspore than there was from the other three or from microspore mother cells—at any rate in some plants. Both these conclusions evidently bear on Thompson's results, but before discussing them some further results must be mentioned.

Sax (1928) gave counts for reciprocal crosses between *vulgare* × *durum* F_1 and the *durum* parent; some made from root tips, and some from pollen mother cells in aceto-carmine. The different counts agree on the whole, and only the totals are given below:

	Proportion of gametes with 14 to 21 chromosomes								No. of counts
	14	15	16	17	18	19	20	21	
♀	0·41	0·20	0·16	0·09	0·07	0·02	0·03	0·02	103
♂	0·57	0·20	0·05	0·04	0·07	0·04	0·00	0·04	56

He concluded from these figures that "loss of univalents, selective elimination of gametes, and possibly selective fertilisation, do not seem to be adequate to account for the great excess of 14 chromosome gametes" and suggested that "it is possible that univalents are frequently eliminated in early embryonic development." The figures are similar to those given by Thompson; and if, as with those, we make the utmost allowance for elimination by sterility, we get an even greater discrepancy than in Thompson's. The two series of results therefore agree; though Thompson has given evidence that this excess of 14 chromosome egg cells occurs only in certain crosses. In view of the existing uncertainty, further study is needed; but unless there is some unrevealed experimental error it seems that we must admit that, in some crosses, there is either (1) loss of chromosomes during early embryonic divisions, or (2) a heavier chromosome loss on the female side than on the male, as well as a departure from random segregation of univalents on the female side. The latter interpretation seems to me preferable and will be considered further.

The gametes formed, if univalents segregate at random and there is no loss, have been given above; they are found from the formula $(\frac{1}{2} + \frac{1}{2})^7$. Loss of univalents would give a distribution of the same form, a binomial one, but gametes with 14 chromosomes would be more frequent, those with 21 less so; and the greatest number would have, say, 16 or 17 chromosomes instead of 17 or 18. If segregation is not random, and there is no loss, there would be equal numbers of 14 and 21 chromosome gametes, but these would be more frequent and those with intermediate numbers would be less so. If, in addition, there is loss, those with 14 would outnumber those with 21 to a greater or less extent according to the amount of the loss. In the microspore mother cells the loss can be observed and allowed for, but it would be difficult to find the chromosome numbers of the microspores if segregation were not at random. That it is sometimes not random in megaspore mother cells is indicated, I think, by the evidence just discussed; but from what is known of other plants (*e.g. Rosa*, Täckholm, 1922) it is quite possible that this happens only on the female side. Also we have seen (p. 223) that the only available evidence suggests that loss of chromosomes is heavier in the female than in the male. If, therefore, we compare the frequencies of functional

male and female gametes by back-crossing the F_1 we cannot be certain that any difference between them is due to sterility. However, since in most F_1's the egg cells are all functional, we can probably take the frequency of female gametes found by back-crossing as being the same as that of the megaspores. If this be so, the high frequency of 14 chromosome egg cells found by Thompson and Sax suggests that there actually was, in their crosses, a greater chromosome loss in the female, as we suggested; as well as a departure from random segregation in the female. The possibility that segregation is not random in the male should also be borne in mind, though this is less likely.

We cannot come to a definite conclusion on the points discussed until a great deal more work has been done, but something must be said of the possible bearing of these results on our previous conclusions concerning the frequency of sterile combinations and on pollen sterility. The proportion of sterile combinations appearing in F_2 would be considerably reduced both by departure from random segregation and by a heavy loss of chromosomes in the female; and the latter factor would decrease the proportion coming from plants with less than 35 chromosomes. On the other hand, the proportion coming from plants with more than 35 chromosomes would be increased by a greater chromosome loss, since in this case the sterile combinations come principally from gametes with low chromosome numbers; and it would not be altered much if segregation were not at random, since this factor increases the proportion of gametes with low chromosome number as well as those with high. The arguments brought forward (Watkins, 1924, 1925) to show that there was a tendency for pollen with intermediate chromosome numbers to be eliminated are therefore not altered in the case of plants with more than 35 chromosomes; and the factors under discussion were not considered at the time for this reason. Neither Nishiyama's (1928) nor Kihara's evidence from crosses between 41 and 42 chromosome plants is in any way affected. Hence it seems fairly certain that pollen having 21 chromosomes is favoured in comparison with that having 20, 19 or 18; but the evidence for a weakening of pollen with 15, and perhaps 16, chromosomes in comparison with that with 14 is less certain.

(*h*) *Conclusion.*

It may perhaps be said that, if one thing has come out more clearly than another from the foregoing discussion, it is the difficulty and uncertainty of the subject; and it will be useful to give a summary of the conclusions.

In crosses between species of the second and third wheat groups the F_1 is partially sterile, and gives at reduction 14 bivalents + 7 univalents; and it is assumed that the 14 chromosomes of the former have paired with 14 from the latter. The 7 univalents divide longitudinally in the heterotype, and appear to segregate at random in the homotype, while loss may occur at either division. The gametes may consequently be expected to contain any number of chromosomes from 14 to 21.

In most F_1's practically all the egg cells can be fertilised by parental pollen, but some of them fail to become fertilised with F_1 pollen. Germination of F_1 pollen on F_1 stigmas is low, but seems to be high enough for fertilisation to occur, so that the exact reason why some egg cells are not fertilised is not clear. Some F_2 and F_3 plants show the same phenomenon, but it is possible that, in the more sterile plants, an added cause for failure to give grain is that egg cells are non-functional, or that embryos abort, though there is so far no definite evidence on these points.

There is a tendency towards suppression of pollen with intermediate chromosome numbers. It is almost certain that pollen grains with 21 chromosomes are more favoured than those with 20, 19, and perhaps 18 and 17; but it is less certain that those with 14 are more favoured than those with 15 and perhaps 16.

Grain germination depends chiefly upon the chromosome composition of the endosperm. It is good if the extra chromosomes of the *vulgare* group are diploid or triploid in the endosperm, but bad if they are only haploid. It is possible that in some cases the chromosome composition of the embryo determines germination, but there is no definite evidence to this effect.

Nearly all plants of F_2 and later generations belong to one of two groups: (1) with from 28 to 35 chromosomes, giving 14 bivalents + 0...7 univalents; (2) with more than 35 chromosomes, and here the sum of the bivalents and univalents = 21 (*e.g.* 18 bivalents + 3 univalents). When plants with other combinations, which are called sterile combinations, appear (*e.g.* 15 bivalents; 18 bivalents + 2 univalents) they are dwarf and sterile or nearly so; and it seems probable that plants which die before an ear is formed have a similar constitution.

Self-fertilisation of plants with more than 35 chromosomes gives plants with an equal or greater number; while those with fewer than 35 give plants with an equal number or less. These two facts are a consequence of the absence of the sterile combinations.

There is evidence suggesting that in F_2 from some crosses far more plants have 28 chromosomes than would be expected, and the dis-

crepancy is too great to be explained by sterility in any or all of its forms. Analysis of the available data suggests that this is partly due to a greater loss of chromosomes at reduction in the female than occurs in the male, and partly because univalents do not segregate quite at random in the homotype in the female—for the male there is no evidence against random segregation. But a different explanation has been suggested, viz. elimination of chromosomes in the early embryonic divisions.

There appear to be several reasons for the rarity of the sterile combinations of chromosomes. Loss of univalents at reduction helps to make them infrequent among the progeny of plants with less than 35 chromosomes. In all cases they would be rendered less frequent by elimination of pollen with intermediate chromosome numbers, and this seems to be the most important factor in reducing their frequency among the progeny of plants with more than 35 chromosomes.

Both of the factors suggested in the last paragraph would help to reduce their frequency in F_2.

While these are the general principles that apply to the pentaploid hybrids it should be realised that their application in different cases is likely to vary. A factor that is important in one case may be less so in another. Thus, chromosome loss is likely to differ in frequency in different cases, and one extra chromosome may have considerable effect on pollen viability while another has little. In illustration, the difference between the two plants studied by Nishiyama (p. 220) should be noticed.

(4) THE GENETICS OF PENTAPLOID WHEAT HYBRIDS.

Pentaploid wheat hybrids have long been studied by plant breeders and genetic workers, since they are comparatively fertile; while hybrids of diploid with tetraploid or hexaploid wheats are almost entirely sterile. As might be expected, they have proved very difficult to analyse; and except for a few characters such as rough and smooth chaff or bearded and beardless ears, which give approximately 3 : 1 ratios, the F_2 is almost impossible to classify. New characters and new types appear in proportions that do not suggest any simple Mendelian ratios. Some characters are found only in association with certain others, while most occur in so many intermediate forms that classification is hardly possible, and F_3 makes the situation no clearer. In general, apart from sterility, the most striking features are the appearance of new and abnormal types in large numbers, and an increase in the variability of many characters, which are found in F_2 beyond the limits set by the parent forms. Vavilov and Jakushkina (1925), describing crosses between *persicum* and a

number of wheats from the third group, besides commenting on the monstrous forms that appear conclude that "decrease and increase in the intensity of the characters, comparatively seldom observed on crosses within the limits of one genetical group of species, in this case becomes a frequent occurrence." Indeed the whole type of inheritance in such crosses is summed up by these authors as "Naudin" type, or "disharmonious," segregation, as distinct from that of Mendel and Wichura "peculiar to closer inter-species crosses." But, though ratios are apt to be irregular, even in the case of the simpler characters for which the crosses can be classified accurately, it is, in my opinion, misleading to make such a distinction; and it has been shown that an accurate analysis of these crosses on Mendelian lines is possible, though difficult.

For economic reasons the crosses are important because of the frequent wish to transfer to *vulgare*, for example, a character that is most highly developed among 28 chromosome forms, such as rust resistance; and genetically they are interesting, not only for the apparently unusual type of inheritance, but also for the light they throw on the relationship between the two groups of species. The primary reason for their unusual features was provided, of course, by Sakamura's discovery that the groups in question differ in chromosome number, and since then they have been studied by a number of workers. Since the F_1 gives 14 bivalents + 7 univalents it has usually been assumed that the 14 chromosomes from one parent have paired with 14 from the other, leaving unpaired 7 specific chromosomes from the *vulgare* group parent; and for the present we will accept this. The members of the bivalents segregate normally, so that any characters determined by them alone should give the usual Mendelian ratios, and should be transferable from one wheat group to the other; but any character determined solely by the unpaired chromosomes should be confined to segregates with the high chromosome number, and therefore to the *vulgare* group, unless such a chromosome does occasionally pair with an Emmer chromosome. This reasoning has been apparent to most workers on the subject; but systematics teaches us that very few characters are actually associated with chromosome number, so perhaps few characters will prove to be determined only by the unpaired chromosomes, and the reasoning in question may have only a limited application.

What is certain is that, as in systematics so in the hybrids, there is association between chromosome number and type. This is different from an association of chromosome number with single characters, and may

have a somewhat different significance, but the two phenomena must to some extent be dealt with together, since some authors have insufficiently distinguished between them.

Sax (1923) made aceto-carmine counts for 15 F_2 and 46 F_3 plants from *durum* × *vulgare*. The numbers given are the sum of the univalents and bivalents, since it was often found difficult to distinguish these, and vary therefore from 14 to 21; "it was also difficult in many cases to get the chromosome count more accurate than ± 1" and "the few plants with counts of 15 or 20 were classed as 14 or 21 respectively." The method then was to work out the correlation (expressed as a correlation coefficient) between chromosome number and the characters "head type," "keel shape," "spikelet shape," "head shape," "diameter of culm," and "rust resistance"; the material being 38 F_3 plants, from 25 families, and classification usually into *vulgare*, intermediate or Emmer. It was found that all five characters were highly correlated with chromosome number and it was therefore thought that "the 7 additional chromosomes of the *vulgare* parent determine the distinguishing characters of the *vulgare* wheats"; but as L. A. Sapehin (1928) has pointed out, though perhaps too sweepingly, "there are no particular species characters. Therefore the view that in the univalent chromosomes are contained some specific genes of *vulgare*, is erroneous." We shall see later that many of the characters are probably affected by both paired and unpaired chromosomes.

Sax and Gaines (1924), working on *durum* × *vulgare*, besides giving evidence that some characters segregate normally and others do not, studied chiefly the practical problem whether important economic attributes of different groups can be combined. They regard this as difficult, but not impossible. An interesting conclusion is that characters are associated more closely in crosses that are more sterile than in those that are relatively fertile; but, in my opinion, we know too little about the mechanism of sterility or of inheritance in these crosses to explain this properly.

Kihara (1924) has given a number of observations on the association between type and chromosome number. In *polonicum* × *Spelta*, for example, he found that 42 chromosome progeny were of *Spelta* or *Spelta*-like type, and 28 chromosome progeny of *polonicum* or *polonicum*-like type; and in general "Der Habitus der 28-chromosomigen Nachkommen dieser pentaploiden Weizenbastarde ähnelt meistens mehr oder weniger dem Emmertypus, während die 42-chromosomigen typischen oder annähernd typischen Dinkel-Habitus besitzen."

Association between chromosome number and resistance to rust has been dealt with by Tochinai and Kihara (1927); the observations referring principally to *Puccinia triticina* and to a less extent to *P. graminis*. For the cross resistant *durum* × susceptible *vulgare* about 80 accurate counts were made, principally in F_4, the majority giving 28 chromosomes; "counts were made through all stages during the maturation division, especially in the metaphase and anaphase of the first division, and if these counts did not coincide with one another, the chromosome number of these plants was regarded as unknown." Usually 28 or 29 chromosome plants were in differing degrees resistant, but were occasionally susceptible; and all plants with high chromosome number were susceptible. In another cross, moderately resistant *polonicum* × susceptible *Spelta*, the 42 chromosome segregates were stated to be far more susceptible than the susceptible parent. It was concluded that resistance to rust is "weakened by the presence of genes existing in" the extra 7 chromosomes from the *vulgare* group parent. Morphological characters were also said to be associated with chromosome number in *durum* × *vulgare* but no details were given except that "pithiness of straw does not ever occur in the plants belonging to the 'Vermehrungsgruppe.'"

Thompson (1925) observed 13 characters in *durum* × *vulgare*, each character being put into one of five classes from *V* (*vulgare*) to *D* (*durum*), and each having some systematic value. The F_2 plants fell into three classes: (1) with chiefly *V* and few or no *D* characters, (2) with chiefly *D* and few or no *V*, (3) with approximately equal numbers of *D* and *V*; class (3) showing high sterility, classes (1) and (2) much less. That the characters were associated was concluded partly from correlation coefficients; and partly because the plants in class (3) were very few in comparison with the expectation from random assortment of 13 characters. The strongest association was between characters "which are always or nearly always characteristic of the species." It is, perhaps, doubtful whether as many as five classes are advisable for a character such as bearded or beardless which depends upon a single factor, but there is no doubt that the number of plants found in class (3) was surprisingly small. The possibility of ordinary linkage was not, unfortunately, considered; and there is no doubt that much of the association between characters came from this cause. The characters "compactness," "keel," "glume shape," "collar" and "beards" are all linked completely or partially (Watkins, 1928); and it is probable that the character "middle tooth" is affected either by one of these factors or by another belonging to the same linkage group. Nevertheless, some of the association must

be due to other phenomena; and it was found in fact, from a number of approximate counts, that many of the characters were associated with chromosome number. The counts are given as numbers from 14 to 21, and unfortunately their meaning is not explained except that they were made "in many cases at both heterotypic and homotypic division." Special attention was paid to rust resistance (the *durum* parent being more or less resistant and the *vulgare* parent susceptible), which was found to be strongly correlated with *durum* characters; but it appeared to be possible to transfer the character from one species to the other since three *vulgare*-like plants were resistant, though less so than the *durum* parent. Recognising the difficulty of finding characters that distinguish the species absolutely it was concluded that to assign *vulgare* characters to the extra *vulgare* chromosomes was too sweeping.

In *turgidum* × *vulgare* also (Watkins, 1927 *a*) although few characters define the species, and valuable characters such as the presence or absence of a keel can be transferred by crossing, it was concluded that a relation between type and chromosome number was quite definite. It was pointed out that one reason for this is that a character such as solid or hollow straw may be associated with chromosome number in the cross—only hollow-strawed 42 chromosome types being extracted—despite the fact that solid strawed *vulgare* wheats exist; and it is probably often the case that a character which is rare in one group, though not quite absent, and common in the other cannot usually be transferred by crossing. Crosses between F_1 and *vulgare* gave (1) plants with more than 35 chromosomes, of *vulgare* type and having only *vulgare* type offspring, and (2) plants with 35 chromosomes which, like the F_1, have offspring of *turgidum* and of *vulgare* type; on the other hand, crosses between F_1 and *turgidum* gave (1) mostly plants of *turgidum* type which have only *turgidum* type offspring, and (2) a few 35 chromosome plants as before. Given an association between chromosome number and type, this behaviour will be readily understood from what has been said about the cytology of these hybrids. It was also concluded that 14 chromosome pollen carried mainly *turgidum* characters, and 17–21 chromosome pollen mainly *vulgare* characters; though the characters to which this conclusion refers were actually few—solidity of straw, ear density, and various features of the glume shape—and the number of plants examined was small enough to admit the possibility of exceptions.

The results described have dealt with two separate phenomena: the association of chromosome number with single characters; and the association between chromosome number and type, or shape, that is with

the way in which characters are combined. That the distinction is important can be illustrated by the cross *turgidum* × *vulgare* (Watkins, 1927 *b*). In this cross the single pair of characters keeled or rounded glume has no association with chromosome number, either being readily transferable from one species to the other; but if the keeled character is taken from *turgidum* to *vulgare* various other characters go with it, and produce a special type—the type speltoid with thick tough glumes and a number of other characters—which is associated with the high chromosome number of *vulgare*. Thus the character keeled glume is not associated with chromosome number itself but it gives, in conjunction with other characters, different types of glume which are so associated.

Of single characters, resistance to rust (*P. graminis* or *P. triticina*) has been studied most; and it seems that in general the cross resistant 28 chromosome × susceptible 42 gives resistant 28 and susceptible 42 chromosome segregates, probably with occasional exceptions (Tochinai and Kihara, 1927; Thompson, 1925; Hayes, Parker and Kurtzweil, 1920; Aamodt, 1927). No doubt this is most easily explained by assuming that the extra chromosomes carry a factor which increases susceptibility; and that the exceptions arise from occasional pairing between this chromosome and an Emmer chromosome. There may be a few other characters, *e.g.* solid and hollow straw, which behave in similar fashion in some crosses (Thompson, 1925; Watkins, 1927 *a*), but in general this type of behaviour is probably rare, and caution must be used in drawing conclusions from it.

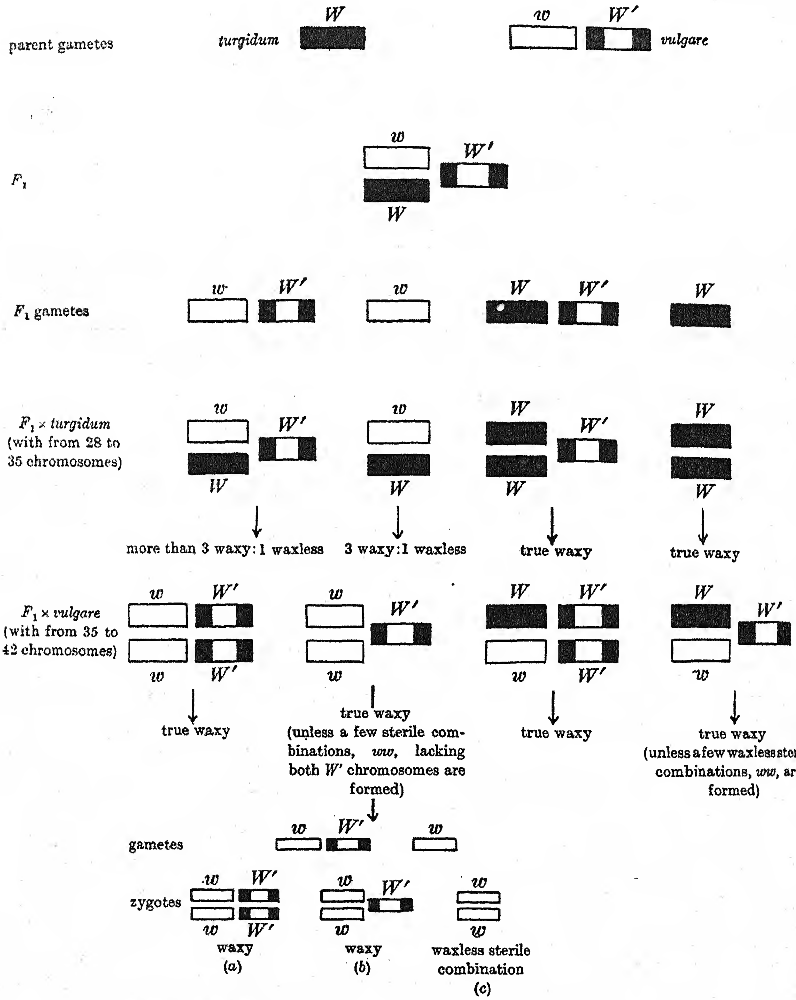
The clear association between chromosome number and type or shape—combinations of characters—forms an interesting genetical problem; but unless care is taken it may give us misleading views on inheritance. It is true that species are types, so that there is a natural tendency in species crosses to try and work out the inheritance of types rather than of single characters; but this will almost certainly lead to errors unless the greatest care is taken over classification—indeed errors of this sort occur in the literature under review. In any case we cannot tell without further evidence whether the association is the result of sterility, in some form or other, or whether, and to what extent, it is due to the factors carried by the extra chromosomes; nor can we conclude that certain characters are determined by the extra chromosomes alone.

Before dealing with these crosses from a somewhat different angle we must describe one further case which shows certain special features: the cross *dicoccum* × *vulgare* (Thompson and Hollingshead, 1927) referred to already. We saw that in this cross there is a preponderance

of low chromosome numbers in F_2—out of 28 plants counted no less than 6 having 28 chromosomes and only 2 having more than 35—and would therefore expect, as proved to be the case, a large preponderance of *dicoccum*-like segregates. Observations were made on 20 pairs of single characters of which a few referred to shape. It was found that they fell into two classes: (1) 6 characters in which nearly all the segregates resembled *dicoccum*; (2) 14 characters in which the segregates might resemble either parent. The characters in the first class were said to be of taxonomic importance, while those in the second were mostly not. The results do in fact show striking differences in the way the characters behave, though the distinction between the two classes is not very sharp; but it does not seem to me altogether certain that there is a difference in the systematic value of the characters in the two classes. It might perhaps be concluded from the results that characters in class (1) are determined chiefly by the extra chromosomes, and those in class (2) chiefly by the segregating chromosomes; but this would not be correct. "Conditions not existing in either parent, for example, the middle tooth prolonged into a short awn, or a pointed lateral tooth, were found in a few segregates. The condition was classed as that which it resembled most." These characters must have depended upon more than one factor, and therefore may have been affected by both paired and unpaired chromosomes.

We will now consider the question of a factorial analysis, taking *turgidum* × *vulgare* (Watkins, 1927 *b*). It will be realised that the problem is difficult, but an exact analysis is theoretically possible since the back-cross ♀ F_1 × ♂ 28 chromosome, at any rate in many cases, gives no appreciable disturbance from sterility: all the egg cells are fertile; and all the grains germinate and give mature plants. The general type of inheritance is best illustrated by the characters waxy and waxless. In the cross in question both parents were waxy, but waxless plants appear in F_2. All such plants are of *turgidum* type. ♀ F_1 crossed back to *turgidum* gives all waxy plants, waxy being dominant, but of these only half breed true to waxy while half split up into waxy and waxless; showing that the F_1 is heterozygous for a single pair of factors, **W** and **w**, for waxy and waxless. On the other hand, F_1 crossed back to *vulgare* gives only waxy plants which breed true to waxy, showing that the extra chromosomes of *vulgare* introduced an additional waxy factor **W′**. It will be convenient to consider the case in greater detail (Diagram 2). The explanation suggested was that the *turgidum* parent was (**WW**), the *vulgare* parent (**ww**) **W′W′**, and the F_1 (**Ww**) **W′**; where

factors enclosed in brackets are carried by chromosomes that pair and segregate normally in the F_1 and **W′** is carried by one of the unpaired



In F_1 × *vulgare* (*ww*) *W′* has more than 35 chromosomes; most of its progeny are (*a*) or (*b*), and (*c*) is the sterile combination. If (*ww*) *W′* had less than 35 chromosomes most of its progeny would be (*b*) or (*c*), and (*a*) would be the sterile combination.

Diagram 2. Inheritance of waxy and waxless foliage in *vulgare*, (**ww**) **W′W′** × *turgidum* (**WW**).

chromosomes; and it will be seen from the diagram that the experimental results given above will follow from this formula. If pairing between **W** and **w** is regular, the F_1 gametes will be formed in the

proportion 1 (**wW**′ + **w**) : 1 (**WW**′ + **W**), and F_1 × *turgidum* will give a 1 : 1 ratio as observed. This ratio would be disturbed if pairing is not regular. The ratio obtained by selfing (**Ww**) **W**′ would depend upon how often the univalent chromosome carrying **W**′ is lost and related causes. It will be noticed that the zygotes (**ww**) **W**′ behave differently according to whether they have less than 35 or more than 35 chromosomes. In the former case a complete set of 7 extra chromosomes is not present, so that (**ww**) **W**′**W**′, in which the extra chromosome **W**′ is bivalent, would be a sterile combination. In the latter case some of the extra chromosomes are bivalent and all 7 must be present for a fertile combination to be formed, so that (**ww**) would be a sterile combination.

The numbers actually found for the ratio waxy : waxless in crosses between F_1 and *turgidum* were 17 : 17, and since they are small we cannot deduce that pairing between *vulgare* and *turgidum* chromosomes was perfectly regular; but for the characters keeled and rounded glume bigger numbers are available, 35 : 34 (Watkins, 1928), so that a fair degree of regularity can be assumed. It will be realised, however, that if autosyndesis occurred **W**′ would pair with **w**, **W** would remain unpaired, and a 1 : 1 ratio would again be obtained. It is clearly difficult to decide between the two possibilities, and further study is to be desired. The question cannot profitably be discussed in detail here but it may be stated that the available evidence—the 1 : 1 ratio, taken in conjunction with the rarity of trivalent chromosomes (Kihara and Nishiyama, 1928), and the fact that the parent forms are regained in a high proportion of cases after back-crossing (Watkins, 1927 *a*)—suggests that allosyndesis is usual in these crosses.

Waxless *durum* wheats are common in cultivation, and crossed with *vulgare* would probably give only waxless *durum* and waxy *vulgare* segregates. In this cross, therefore, the character waxless would be associated with *durum* although not characteristic of that species.

Although the inheritance of waxy and waxless was not worked out in as much detail as could be wished, some such formula as the one put forward seems fairly certain. A similar formula was suggested, but on less certain evidence, for the characters resistance and susceptibility to *Puccinia glumarum*—namely, parent *vulgare* = (**pp**) **P**′**P**′, and parent *turgidum* = (**PP**)—and again in a further case that must be described in detail. Waxless is an example of a new character which first appears in F_2 and is confined to segregates with a low chromosome number. The case to be considered now is the appearance of two new types, one confined to segregates with a low chromosome number, and the other to

those with a high one (Watkins, 1927 *b*, 1928); the principal characters involved being the glume keel, glume thickness, and laxity of ear. It was first thought (1927 *b*) that all the characters were controlled by a single factor **K**, but the later view (1928)—that **K** might represent a group of completely linked factors—now seems to me more probable. The *turgidum* parent, which has a keeled glume of normal thickness and a moderately dense ear, has the formula 28 chromosomes-**KK**; and the *vulgare* parent, with round glumes of normal thickness and an ear that is also moderately dense, the formula 42-**kk**; where **K** gives the keel to the glume, increases the thickness of the glume, and increases the laxity of the ear, and **k** is its allelomorph. By crossing, we obtain the two new types 42-**KK** and 28-**kk**; the former being the type known as speltoid—a *vulgare* type with a lax ear and thick, keeled, glumes that are only pulled away from the grains with difficulty; while the latter is a very dense-eared *turgidum* with thin, rounded glumes. The evidence for this interpretation seems conclusive. Speltoid (42-**KK**) × *vulgare* (42-**kk**) gave a 1 : 2 : 1 ratio in F_2; speltoid × *turgidum* (28-**KK**) gave only keeled plants—speltoids, *turgidum*, and a series of intermediates between them; and *turgidum* × *vulgare* F_1 (35-**Kk**) gave a 1 : 1 ratio for **K** : **k** when crossed back to *turgidum*. Finally, by comparing the types 28-**kk** and 42-**kk**, or 28-**KK** and 42-**KK**, and by other similar evidence (Watkins, 1928), it was concluded that the effect of the extra chromosomes was like that of **K** itself; and it was therefore suggested that one of them carried a group of linked factors, **K′**, similar to **K**. The formulae of the *turgidum* and *vulgare* parents would therefore be (**KK**) and (**kk**) **K′K′** respectively (see also later, p. 239).

Apart from the fact that the keel of the glume has some value in systematics, the interest of the case is first the explanation it gives of the appearance of two new types, each associated with a different chromosome number. Secondly, that owing to the great differences between round glumed *turgidum* and *vulgare*, or between *turgidum* and speltoid—differences that are no doubt largely due to the extra chromosomes—it could not have been predicted from the appearance of the two 28 chromosome forms that the genetical difference between them was the same as that between the two 42 chromosome forms; and it was suggested that, in general, the variation within allied species may often be due to similar genetic differences even when this is not at first apparent. It should be mentioned that the dense-eared, round-glumed *turgidum* or *durum* types that come from crossing these species with *vulgare* have often been erroneously referred to in the literature on such

crosses as *compactum* types, or as dense-eared *vulgare* types; the reason being that a rounded glume is not usually found in wheats of the Emmer group.

Later (1928), formulae were suggested to express the relation of the *vulgare* and *turgidum* forms to other wheat types. In addition to **k**, **K** and **K′**, the formulae involved $\mathbf{K_S}$, which was related to **k** and **K** as if the three were multiple allelomorphs, but it was considered possible that each was really a group of linked factors.

From the results just given we can follow the general principles of inheritance in these crosses; but a disadvantage of the method is that only a small number of plants could be studied, so that exceptions and complications may have been missed. This contrasts with the work of the Sapehins (1928) who continued to F_7 a *durum* × *vulgare* F_2 consisting of 284 plants, several hundred thousand plants being examined in all. The method of investigation was to study separately the *durum*-like and *vulgare*-like segregates for a number of generations; classification being carried out by comparing each individual with a standard scale of ear types (A. A. Sapehin, on *vulgare*-like plants) or glumes (L. A. Sapehin, on *durum*-like plants). In the scales were 35 and 61 types respectively. Simple Mendelian segregation was observed, but segregation occurred "mostly in regard to types, to complexes of genes." Apparently, a factorial analysis was not attempted; but since the types were followed for several generations considerable insight into the principles of segregation was gained.

It was found that many characters could be transferred from one species to another; for instance glume characters, as noted above (p. 236). Presumably, from the results of other workers the [illegible]erved transference of characters such as rust resistance and h[illegible]w was only of rare occurrence, but this is not stated. Segregates combining certain valuable *durum* properties with the general features of *vulgare* were obtained. As we have mentioned, many of the characters segregated in linked groups; thus, when the *durum* segregates were classified by glume shape it was found that many characters went with this feature. But "the presence of rare exchanges makes us suppose that every such combination of characters depends on several genes closely linked with one another." Only combinations of characters were associated with chromosome number.

These results support the possibility that **k**, **K** and $\mathbf{K_S}$, mentioned above, are actually groups of linked factors.

We are now in a position to draw certain conclusions about inheritance

in these crosses. First, some characters, such as hollow straw and rust resistance, are usually associated with a high or a low chromosome number. Others—even important features of the glume shape—are easily transferred from one species to another. Secondly, new characters appear, and there is a general tendency for variation to exceed the limits

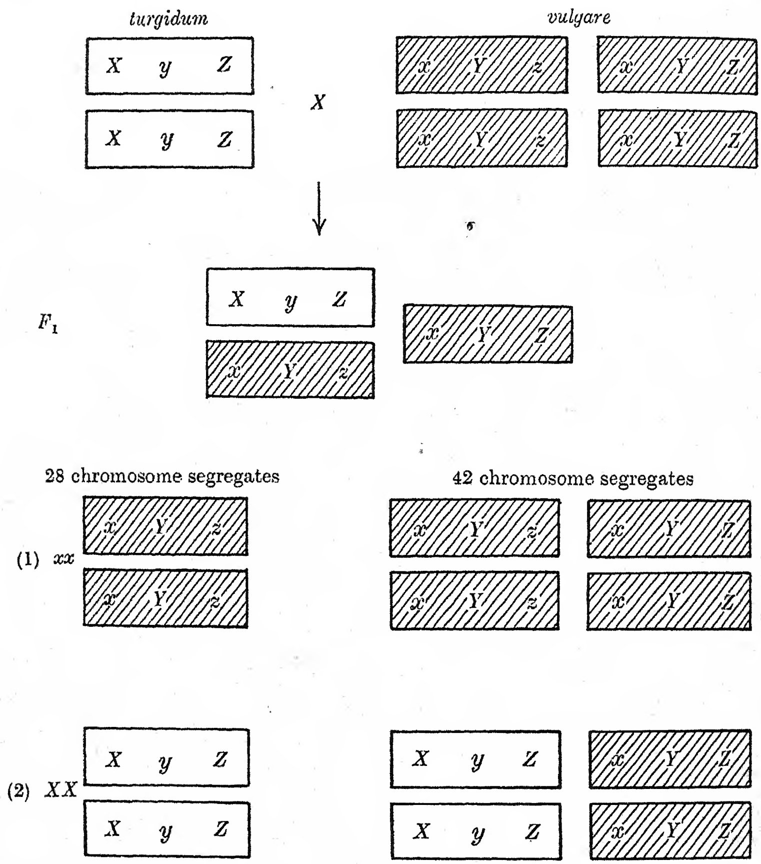


Diagram 3. Example of the association of type with chromosome number. The character determined by X is transferable from one species to another. But the type is associated with chromosome number, since the 42 and 28 chromosome segregates will differ by Z if both are xx, and by Y if both are XX (*vulgare* chromosomes shaded).

set by the parents. Thirdly, many characters segregate in groups, and these groups are probably determined by groups of factors, since an occasional separation of the characters has been reported. Finally, there is a definite association between chromosome number and type, *i.e.* combinations of characters.

All these facts evidently agree with the factorial composition deduced above (p. 233), namely, that the paired and unpaired chromosomes carried a similar series of factors, *turgidum* gametes carrying A_1 and *vulgare* a_1A_2. The former species being tetraploid and the latter hexaploid we should expect them to contain, respectively, two and three similar series of factors; and if this is so the formulae should be A_1A_2 and $A_1a_2A_3$. Introduction of the third factor is not necessary to explain the results but is preferable for the reason just given. We will assume throughout that A_3 is carried by an unpaired chromosome. Then in the cross $a_1a_2 \times a_1a_2A_3$ the character determined by these factors would be associated with chromosome number absolutely unless there is occasional pairing between A_3 and another chromosome.

In $a_1A_2 \times a_1a_2a_3$ the character would be transferable.

In $a_1A_2 \times a_1a_2A_3$ we should obtain the new character given by a_1a_2. In the same cross we should obtain $a_1A_2A_3$ in which the character might be more highly developed than in either parent; and there would be similar occurrences in most of the possible crosses, *e.g.* $A_1a_2 \times A_1A_2a_3$.

Finally, if A_1, etc. represent different groups of linked factors, *e.g.* $A_1 =$ **wXyz** and $A_2 =$ **WXyZ**, etc., we shall have an association between type and chromosome number. This was actually worked out of course in the case of the new type speltoid, where the cross **K** × **kK′** gave the new types **k** and **KK′**. If **K** and **K′** are different all four types would be associated with chromosome number. An illustration of such a case, wherein the combination of characters is associated with chromosome number although the individual characters are not, is given in Diagram 3. If X and x in the diagram represent the characters keeled and round then these characters are transferable; but the two round glumed types (round glumed *turgidum* and parent *vulgare*) will differ in other characters, as will the two keeled types (parent *turgidum* and speltoid). The characters actually involved are ear density and glume thickness, but at this stage these characters cannot be defined factorially since the available evidence refers only to the groups A_2 and A_3, and A_1 requires to be known as well.

The formulae found for the characters waxy and waxless, and for keeled and rounded glume, therefore explain the general features of inheritance in the crosses we have been considering. The crosses will have to be worked out much more fully, and some characters may prove to be inherited in a different manner, but it seems fairly certain that many characters are inherited along some such lines as those suggested. A method of attack has been provided, but complications probably exist.

We can also understand more clearly why members of the different

groups are usually distinguished by differences in degree rather than kind, or by the way in which characters are combined.

(5) The origin of speltoid mutants.

Speltoid mutants appear sporadically, as mutants or as chimaeras, in cultures of *T. vulgare*; and are interesting from their curious genetic behaviour as well as from the theories suggested to explain their origin. Their genetics, and that of the related forms, is very complicated and it will probably be best to discuss them in relation to Winge's theory (1924) that they arise from the irregular pairing of chromosomes at reduction. Winge pointed out that the gametes of the hexaploid *T. vulgare* should be regarded as having $7 + 7 + 7$ chromosomes, of which one set of 7 is not very different from another. If a chromosome from one of these sets be called A, then the other two sets will contain chromosomes B and C not very different from A. Considering only these chromosomes, that is one from each set of 7, *vulgare* will have the formula $\frac{ABC}{ABC}$; and it is suggested that, because of their similarity, B and C may sometimes pair at reduction instead of B always pairing with B and C with C, as they should; so that $\frac{ABC}{ACB}$ would form the new gametes ABB and ACC. The former meeting the normal gamete ABC, would give $\frac{ABC}{ABB}$ which, it is supposed, is the mutant form, the heterozygous speltoid.

In support of this view Winge found that, in a heterozygous speltoid with 42 chromosomes, but not in the normal form, a trivalent and a univalent could be seen. These, he considered, were BBB and C. In the homozygous speltoid, which would be $\frac{ABB}{ABB}$, he gave evidence that a quadrivalent chromosome is sometimes formed. Since, however, heterozygous speltoids may split up into the three types, normal, heterozygote and homozygous speltoid, in widely different ratios, he supposed as well that in some strains the univalent C might be lost frequently and only rarely in others; and, again, that in some strains pollen carrying ABB might tend to be eliminated. The formation of 41 chromosome heterozygotes $\frac{ABC}{AB}$ was also envisaged. In discussing the experimental results in the light of Winge's theory, the great difficulty is that the genetical and cytological investigations have been carried out independently, with the single exception of Huskins' (1927) work on the analogous problem of the fatuoid mutants that are found in the hexaploid oat *A. sativa*, and even here the correlation is not yet completely worked out.

In Huskins' work the most striking feature is the demonstration that

the heterozygous fatuoid may have 41, 42 or 43 chromosomes, and will give different ratios accordingly; so that Winge's subsidiary assumptions to account for the aberrant ratios are in some cases unnecessary. In his type 1 Huskins found that the normal, heterozygous fatuoid, and homozygous fatuoid all had 42 chromosomes. The reduction divisions of the normals were rather more irregular than those of normal varieties, in that univalents were occasionally seen, but 21 bivalents were usual and trivalents were not observed. The heterozygotes could have 1 trivalent + 1 univalent, but it was only rarely that both of these could be seen in a single cell because of the difficulties of observation. Oat chromosomes, like those of wheat, are large and tend to obscure each other. In the homozygous fatuoids a quadrivalent was probably frequent, but it was usually not possible to establish its presence certainly. As would be expected, the heterozygotes of this type give approximately 1 : 2 : 1 ratios, but the ratios are somewhat irregular.

In types 2 and 3 the heterozygote has 41 chromosomes, which give 20 bivalents + 1 univalent at meiosis, and must be regarded as $\frac{ABC}{AB}$. The normal has 42 chromosomes, $\frac{ABC}{ABC}$. The homozygous fatuoid has 40 chromosomes, which may give 20 bivalents at meiosis, but the divisions are usually rather irregular. It only occurs in small numbers and is weak and sterile, being a sterile combination (see p. 208) with the formula $\frac{AB}{AB}$. As would be expected, each type gives fewer normals than heterozygotes, the ratio being in one case about 1 : 1·5 and in the other about 1 : 4.

In type 4 the heterozygote has 43 chromosomes, which usually form 20 bivalents + 1 trivalent but may give 21 bivalents + 1 univalent. It is regarded as $\frac{ABCB}{ABC}$. The normal has 42 chromosomes that pair regularly. The homozygous fatuoid has 44 chromosomes and is dwarf and sterile, being presumably $\frac{ABCB}{ABCB}$. Its divisions are rather irregular, but it was sometimes possible to count 22 bivalents and sometimes 20 bivalents + 1 quadrivalent. The strain gave about 8 normal : 19 heterozygotes : 8 fatuoids. The results are too limited for this ratio to be discussed, but probably it approaches 1 : 2 : 1 because an extra chromosome has less disturbing effect than a missing one.

In these results the cases where the fatuoid type is associated with the gain or loss of a whole chromosome seem convincing; and though the first case, type 1, is clearly much more difficult to establish, there seems no doubt that the chromosome behaviour is different in the three types—normal, heterozygote and fatuoid—and the interpretation given

by Winge and Huskins probably contains a good deal of truth. Huskins has attempted (1928) to explain Nilsson-Ehle's speltoid results (1920, 1921) along similar lines, but before considering these, and the work of Lindhard (1922, 1923, 1927) and Åkerman (1920, 1923, 1927), some preliminary explanations are called for.

The characters speltoid and bearded are associated; beardless heterozygotes giving nearly always only beardless normals, beardless heterozygotes, and bearded speltoids; but a crossing-over of about 27 per cent. has been observed on rare occasions (see p. 247). Presumably the factors involved are carried by the same chromosome, and on the theory outlined above the beardless normal, $\frac{ABC}{ABC}$, carries beardlessness (the dominant) in chromosome C, which may be represented as $\overset{\text{b'less}}{\rightarrow\leftarrow}\!\!\longrightarrow\!\!\overset{\text{norm.}}{\rightarrow\leftarrow}$; chromosome B being $\overset{\text{b'ded}}{\rightarrow\leftarrow}\!\!\longrightarrow\!\!\overset{\text{sp.}}{\rightarrow\leftarrow}$. Since the 41 chromosome heterozygotes segregate because of the segregation of a whole univalent chromosome, complete linkage between the characters bearded and speltoid must follow. But in the 42 chromosome heterozygote, $\frac{ABC}{ABB}$, B can pair with C and the linkage in question should no longer be complete. It is possible, too, that an occasional cross-over might occur in the 43 chromosome heterozygote since the divisions in this form are somewhat irregular, and a trivalent may be formed.

The considerable body of genetic work carried out by Nilsson-Ehle and Lindhard was done entirely without reference to cytology, and interpretation is therefore difficult. The 42 chromosome strains should usually be distinguishable from those with 41 or 43 by the homozygous speltoids, which should be vigorous and fertile in the first case, weak and sterile in the second. Unfortunately, these details do not appear always to have been given. Furthermore, the ratios found have probably often been distorted by winter-killing: Åkerman mentions a survival rate of about 30 per cent., Lindhard (1922, 1927) rates from 17 to 77 per cent. The latter has shown too (1922) that winter-killing falls more heavily, in some strains, on homozygous fatuoids than on normals; while "In anderen Linien kann wiederum der Vulgare-Typus der schwächlichere sein" (1927). Though it is evident from the results that many of the distinctive features of the splitting ratios are not due to winter-killing, there are yet many cases in which uncertainty is inevitably introduced thereby. Finally, Lindhard (1922) has also concluded that natural crossing takes place occasionally: as might be expected from the fact that in 41 and 43 chromosome strains the heterozygotes would be partially sterile and the homozygous speltoids still more sterile. Granting

that crossing is the correct explanation, the cases in question can usually be picked out but uncertainty exists in a few instances.

On the basis of the ratios in which they segregate, Nilsson-Ehle (1921) has divided his speltoids into three types, *A*, *B* and *C*. In type *A* the ratio approximates to 1 : 2 : 1 but the homozygous speltoids are in defect; *e.g.* 42 normal : 81 : 29, and 60 : 81 : 15 (1921, Tables II, XIV); and the homozygous speltoids are, as expected, "verhältnismässig zahlreich und starkwachsend." A strain of this type examined by Huskins (1928) was found to have 42 chromosomes in each of the three forms and split up into 14 normal : 21 : 9. We can be fairly confident that the cases cited by Nilsson-Ehle as belonging to this type really have 42 chromosomes; but, nevertheless, contrary to expectation, linkage between the bearded and speltoid characters is complete in every case. Nilsson-Ehle considers that the departure from a ratio of 1 : 2 : 1 is caused by a partial elimination of pollen carrying the speltoid character.

Heterozygotes of type *B* give very few homozygous speltoids, and the heterozygotes are more numerous than would be expected on a 1 : 2 : 1 basis; *e.g.* 12 normal : 53 : 1 (see 1921, Tables IV–IX). The progeny of a large number of heterozygotes contained about 1 per cent. of homozygous speltoids; a further type, sub-compactum, was found almost as often, and an awned speltoid heterozygote less frequently. In several strains Huskins found that the normals had 42 chromosomes and the heterozygotes 41. The latter formed 20 bivalents + 1 univalent, and were given the formula $\frac{ABC}{AB}$. This evidently agrees with the ratios found for heterozygotes of this type. Since the univalent is sometimes lost 20 chromosome gametes would be formed more often than 21; and almost certainly (p. 226) 21 chromosome pollen would be favoured at the expense of that with 20. The ratios would be expected to fluctuate, as they do, and an excess of 41 over 42 chromosome progeny would be expected. But such a great defect of the sterile combination, the 40 chromosome bearded speltoid, suggests that elimination of zygotes may possibly have been a factor in addition to those discussed earlier (p. 226) —loss of univalents and pollen sterility—which is not unlikely in view of the probable losses from winter-killing. The complete linkage between beardless and normal agrees with expectation. The occurrence of a few bearded heterozygotes may be due to natural crossing or to a pairing between chromosomes *B* and *C* accompanied by crossing-over, as explained later (p. 248). The sub-compactum type will not be dealt with here beyond what is said on p. 250.

The heterozygotes of type C (1921, Tables X–XII) again give very few homozygous speltoids but give more normals than heterozygotes, or sometimes approximately equal numbers of the two classes; *e.g.* 61 normal : 45 : 2, or 61 : 61 : 3. In most cases the three types, A, B and C, are easily distinguished by their different ratios; but occasionally, as Nilsson-Ehle points out, a ratio may leave the matter doubtful, *e.g.* 102 : 188 : 1. In two strains examined by Huskins which split in ratios of 48 normal : 67 : 0 and 40 : 48 : 2, the normals had 42 chromosomes and the heterozygotes 43, while 1 homozygous speltoid had 44 chromosomes. The heterozygotes sometimes gave 20 bivalents + 1 trivalent, but the divisions were somewhat irregular. Their formula is presumably $\frac{ABCB}{ABC}$. One normal, out of four examined, had only 41 chromosomes, and must be presumed to lack a chromosome that has no influence on the speltoid character. The ratios found are again what might be expected from the cytology of the heterozygote; and there is again complete linkage between beardless and normal, except for the occasional production of awned speltoid heterozygotes and awnless speltoid homozygotes, which might have originated as indicated above.

All three types, A, B and C, can originate as mutants from normal plants, and in 1921 Nilsson-Ehle stated that five of each type had been found. On the chromosome view they originated when a normal plant $\frac{ABC}{ABC}$, through irregular divisions, gave gametes ABB, AB or $ABCB$. He also found that a heterozygote of type C (43 chromosomes) could throw one of type B (41 chromosomes); a line throwing excess of normals suddenly giving a plant that throws excess of heterozygotes (see especially 1920, Table II). On the chromosome theory this is not unexpected, since the rather irregular divisions of the 43 chromosome heterozygote, $\frac{ABCB}{ABC}$, might easily give a 20 chromosome gamete AB. Nilsson-Ehle observed this several times; but he also concluded, though only on two occasions out of 260, that type B could give type C (1921, Table VIII, no. 1917–384, and Table XIII, no. 1920–514). This is less likely on the chromosome theory since it demands that the 41 chromosome type $\frac{ABC}{AB}$ should have given a gamete $ABCB$, which though not impossible seems unlikely. It should be pointed out, however, that the first of the two exceptional C lines out of B contains two sub-compactum plants, and the other type C families (Tables X–XII) contain none.

A great amount of valuable data has been given by Lindhard (1922, 1923) who carried on for a number of years the progeny of a single mutant that appeared in 1914. The original heterozygote gave 18 normal

(called squarehead by Lindhard) : 54 beardless heterozygotes : 2 bearded heterozygotes. Except that the normals were larger and stronger than the heterozygotes there is no evidence as to whether the latter were 41 or 42 chromosome forms, since the ratio might conceivably have been given by either. Lindhard suggests that the two bearded plants arose from natural crosses, and throughout the experiments occasional aberrant forms appear to have come in this way. The uncertainty that may arise from winter killing has been referred to already, and it should be pointed out that in one winter, which was very severe, the survival rate was only 10 per cent. Lindhard himself showed that a true ratio of about 1 normal : 8 heterozygotes could sometimes become about 1 : 5. With very few exceptions, which are given below, all the lines continued to split in the ratio of about 1 : 5 or 1 : 8 heterozygotes plus a few "compactum type." Homozygous speltoids were not obtained. This suggests that they were all of type *B*, in which the heterozygotes have 41 chromosomes; and that the sterile combination, homozygous speltoid, has been completely eliminated. This view agrees with the fact that ♀ heterozygote × ♂ normal gave a ratio of 14 normal : 195 heterozygotes though the number of normals is rather low; and is not inconsistent with the ratio 103 normal : 0 heterozygotes for the cross ♀ normal × ♂ heterozygote, though complete elimination of 20 chromosome pollen is surprising. On the other hand, in a few exceptional cases, these 1 : 5 lines threw 1 : 1 lines (1923, Tables II and XX); and if both ratios are to be explained on Huskins' theory this demands the unexpected throwing of a 43 chromosome heterozygote by one with 41 chromosomes. In one case an original 1 : 5 line gave a family splitting in the ratio 1 : 1. The heterozygotes of the latter continued to split in this ratio except for one plant which changed back to 1 : 4, and this ratio was continued except by one plant, which went back yet again to 1 : 1. Lindhard suggests that the latter cases may have been caused by natural crossing between lines of different type.

We must now turn to the homozygous speltoids, which appeared in Lindhard's cultures on three separate occasions. In the first case two heterozygotes from a line splitting in the ratio 15 : 65 gave 9 normals : 63 : 14 homozygous speltoids and 6 : 44 : 51. These ratios suggest that the two heterozygotes were 42 chromosome forms, and this is supported by the high weights of the homozygous speltoids split off, since if the latter had come from a line of *B* or *C* type they should have been small and nearly sterile. The original line suggests *B* type, however, so that a 41 chromosome heterozygote $\frac{ABC}{AB}$ must have given two

42 chromosome heterozygotes $\frac{ABC}{ABB}$, a quite possible contingency. In the second case a family of 71 : 474 contained one plant differing somewhat from the rest and giving 2 : 15 : 2 homozygous speltoids. The latter being frail, dwarf-like, and of low fertility, were almost certainly 40 chromosome plants, so that their origin needs no special comment beyond the fact of their parent plant having differed from the rest of the family. The third instance need not be given here.

Apart from a few cases to which attention has been called, we can conclude that Lindhard's results agree with the supposition that his original mutant was of the 41 chromosome type, and continued to split in the expected fashion, but gave occasionally 42 and perhaps 43 chromosome lines. It is, therefore, surprising that the line examined by Winge (1924) was found to have 42 chromosomes instead of 41.

In a later paper (1927) Lindhard gives the results obtained by continuing the line in which homozygous speltoids were first found. It will be recalled that this appeared to be a 42 chromosome line. The ratios form an almost continuous series from 1 : 5, which we have called type *B*, to 1 : 2 : 1, type *A*; *e.g.* 29 : 146 : 0, 28 : 213 : 3, 28 : 193 : 10, 21 : 129 : 17, 15 : 69 : 22. Lindhard's interpretation is that the ratio is affected by a pair of factors **L** and **l**, which also influence the ear density. Thus, he found three types of speltoid heterozygotes: (1) dense eared, **ll**, giving a ratio of about 1 : 8 : 0, and continuing to give this ratio; (2) medium density, **Ll**, giving a ratio of *e.g.* 13 : 63 : 4, and splitting off plants of type (1); (3) lax eared, **LL**, giving a ratio of *e.g* 15 : 149 : 76. It is not certain from the results whether the heterozygotes of (3) continued to give ratios of this type as they should on Lindhard's theory. In the absence of cytological observations it is difficult to interpret these results. Lindhard was possibly dealing with a mixture of cytologically different types—type (1) being perhaps a 41, type (3) a 42 chromosome type, and type (2) perhaps a 42 chromosome type that split off 41 chromosome plants—but, even so, some of his results show that phenomena other than those suggested by the chromosome theory are involved. A good example of this is given by lines that split in a ratio such as 15 : 149 : 76, wherein the deficiency of normals is associated with weak growth.

The segregation observed by Åkerman (1920, 1923, 1927) in his speltoids need not be considered in detail since it was similar to that observed by Nilsson-Ehle. An important feature of his work is that speltoids were often found to arise as chimaeras; and that, consequently, irregular ratios will sometimes be produced by this means. On the

chromosome theory a chimaera would arise from loss of a chromosome at a somatic division.

The different types of splitting found by Kajanus (1923 *a*) also agree on the whole with those of Nilsson-Ehle. The mutants appeared after crossing various *vulgare* wheats, in F_2 and later, and an interesting conclusion is that they appeared to come in definite (small) proportions in the different cases.

It is clear that a great many of the results given above agree with Huskins' theory, but there are also several difficulties: (1) Throwing of C type (43 chromosomes) by B type (41 chromosomes) is reported by Nilsson-Ehle and Lindhard. This is not impossible on Huskins' theory but is unexpected. (2) Most of Lindhard's heterozygotes should have 41 chromosomes but the one examined by Winge had 42. (3) The results attributed by Lindhard to his factor **L** need explanation; but they can hardly be used to contradict the theory in the absence of evidence as to the cytological nature of the strains. (4) The effects of the B and C chromosomes on the plant are not very easily understood. Thus, no differences are described for the ears of the three types $\frac{ABC}{AB}$, $\frac{ABC}{ABB}$ and $\frac{ABCB}{ABC}$, but these are all quite different from the homozygous speltoid $\frac{ABCB}{ABCB}$.

These difficulties will probably be cleared up, but certain facts suggest that, in addition to the factors suggested by Huskins, other phenomena are involved:

(1) The complete linkage between bearded and speltoid in 42 chromosome heterozygotes. Apart from species crosses, in which the crossing-over is about 39 per cent. (Watkins, 1928), the only exception to complete linkage reported is that given by Nilsson-Ehle (1927), who crossed a bearded normal × a beardless speltoid and found a crossing-over of about 27 per cent. It is true, of course, that in this cross it is beardless and speltoid that enter the cross together, and in the mutants it is bearded and speltoid that are completely linked. But this cannot be the reason for the difference in behaviour, since in the F_2 from Nilsson-Ehle's cross some of the heterozygotes are formed of course from the union of bearded speltoid with beardless normal gametes; and the F_3 shows that the expected 27 per cent. crossing-over between bearded and speltoid has occurred in these cases. Evidently there is something in 42 chromosome speltoid mutants which prevents crossing-over in one chromosome, although this is not a necessary characteristic of speltoids.

(2) Both Nilsson-Ehle (1921) and Åkerman (1923) have concluded that there is sometimes a partial elimination of pollen carrying the speltoid character in A type heterozygotes. This may perhaps be due to

the same factor involved in (1) above. That it need not necessarily occur in speltoids of this type is shown by the good 1 : 2 : 1 ratios that are sometimes obtained.

(3) The occurrence of strains in which the normal segregates are weak and in defect (p. 246; Lindhard).

(4) A normal plant must form the gamete *ACC* as often as *ABB*, so that 42 chromosome *compactum* and speltoid heterozygotes should arise equally often. Actually, the former have not been recorded as original mutants. In other cases, too, the chromosome theory postulates gametes for which there is no evidence.

Nilsson-Ehle (1920, 1921, 1927) has offered a different explanation for the origin of the mutants, which, together with his criticisms of the chromosome theory, must now be dealt with. Winge's theory involves a whole chromosome; Nilsson-Ehle's loss mutation affecting a considerable region of one chromosome. He points out that, although total mutations from beardless normal to bearded speltoid are most frequent, he has also had instances of partial mutation—from beardless normal either to beardless speltoid, or to bearded normal, or to half awned normal. Clearly the simplest view is that these are factor mutations as he argues, and it is therefore reasonable to regard the complete change as a complex factor mutation. From the linkage value found, the two factors bearded and speltoid must be situated some distance apart in the same chromosome, and he considers that a complex mutation involves not only these two factors but the factors lying between them as well; and that because the whole region is affected crossing-over is prevented, the pollen carrying the mutated chromosome is adversely affected, and the mutants are in general weaker than the normal plants. But when a beardless speltoid arises it is from the mutation of one factor alone, and crossing-over is then possible. Winge, on the other hand (1924), suggests that part mutations arise from a cross-over between chromosomes *B* and *C*. Thus the normal plant *BBCC*, or

b'ded	sp.	b'less	norm.
→←———	———→←	→←———	———→←
→←———	———→←	→←———	———→←,
b'ded	sp.	b'less	norm.

by faulty pairing

b'ded	sp.	b'ded	sp.
→←———	———→←	→←———	———→←
→←———	———→←	→←———	———→←
b'less	norm.	b'less	norm.

can give the gamete

b'ded	sp.	b'ded	sp.
→←———	———→←	→←———	———→←,

and from this the usual heterozygous speltoid arises. But if crossing-over has occurred at the same time as the faulty pairing then the gametes

b'less sp.	b'ded sp.		b'ded norm.	b'ded sp.
→←———→←	→←———→←	and	→←———→←	→←———→←

would be formed; and from these would come the beardless speltoids and the bearded normals. This explanation would of course cover certain exceptional plants referred to on earlier pages (pp. 243 and 246). Against this explanation Nilsson-Ehle points out that in the 42 chromosome heterozygous speltoid $\frac{BC}{BB}$ crossing-over never, or hardly ever, occurs; therefore the part mutations could not arise in this way. On the chromosome theory, therefore, we have to explain why a mutant produced by pairing between B and C without crossing-over gives no crossing-over in subsequent generations; while a part mutant, produced by pairing between B and C with crossing-over, does give crossing-over in subsequent generations. A strong argument for Nilsson-Ehle's view is, in my opinion, the fact that both half-bearded normal and bearded normal can arise from beardless normal. The simplest view of the relation between the three types is that bearded, half-bearded, and beardless form a series of multiple allelomorphs; indeed they are a typical instance of this phenomenon. If this be granted, then the origin of half-bearded or bearded from beardless is almost certainly an instance of factor mutation. It is not, unfortunately, quite certain. Winge considers that speltoids come from a rearrangement involving chromosomes B and C; B carrying bearded and C beardless. If the third chromosome A carries half-bearded, a rearrangement involving A would make the origin of half-bearded forms possible. I have, throughout this discussion, neglected possibilities connected with this chromosome since their consideration at this stage would add confusion to a subject already sufficiently obscure. Nilsson-Ehle himself, however, does not consider that the three characters are due to multiple allelomorphs, since he finds that crossing-over between bearded and speltoid is about 27 per cent., and between half-bearded and speltoid about 36 per cent. This seems to me to mean that the bearded and half-bearded factors influence the amount of crossing-over; but Nilsson-Ehle concludes that half-bearded is further from speltoid than is bearded, thus

$\frac{1}{2}$ b'ded b'ded sp.
→←————→←————→←,

and that the characters behave genetically like multiple allelomorphs because crossing-over cannot occur in the region between bearded and half-bearded.

In conclusion, it seems to be well established that speltoids can arise from the loss or addition of a whole chromosome; 41 or 43 chromosome forms, which can be readily demonstrated cytologically, being produced. But, paradoxically enough, although this theory was developed as an extension of Winge's, Winge's theory itself is less satisfactory. He supposed that a 42 chromosome mutant arises simply from a mechanical irregularity at the heterotype division; this giving a rearrangement of the existing genetical material, B being substituted for C, and a gamete ABB produced instead of ABC. Cytologically, this is difficult to establish. Partly because it is not easy to prove the existence of a trivalent chromosome in a 42 chromosome wheat, where the large size and numbers of the chromosomes both give difficulty. Partly, also, because the trivalent chromosome in the heterozygote is presumably the result of the change from normal, and does not necessarily show that irregular pairing occurred in the normal itself. As for the genetic evidence, phenomena such as the linkage relations between bearded and speltoid—their complete linkage in 42 chromosome heterozygotes, coupled with the origin of partial mutations—show that Winge's hypothesis alone will not explain the facts. On the other hand, it does bring the origin of 41, 42 and 43 chromosome heterozygotes all into line; while Nilsson-Ehle's theory of factor mutation, although it agrees satisfactorily with the genetical evidence, can only apply to the 42 chromosome forms and would leave their origin quite unrelated to that of the others. For this reason, and because it is a logical development from the polyploid nature of wheat, Winge's theory is attractive; but it will evidently need considerable modification. The diversity of strains isolated by Lindhard, *e.g.* the one with normals of weak growth, indicate that the problem is more complicated than the chromosome theory in its present form suggests[1].

The origin of speltoids not yet being clear I have not dealt with the compactum heterozygotes and other types that have also been found. The valuable data given by Lindhard (1922, 1923) on these forms show that the subject is one of great complexity, and is very important for a proper understanding of the speltoid problem. From its appearance, the compactum heterozygote is evidently the complimentary form to the speltoid heterozygote, namely $\frac{ACC}{ABC}$.

The origin of speltoids in species crosses has no direct bearing on their origin as mutants.

[1] The origin of such strains could be readily explained, of course, if crossing-over between B and C could occur.

(6) INHERITANCE IN CROSSES BETWEEN TETRAPLOID WHEATS.

Two abnormalities have been observed in these crosses. The first, apparent failure to segregate, was reported by Biffen (1916) in a cross between a white chaffed *polonicum* and a grey chaffed *turgidum*. F_1 was white chaffed, almost like the parent *polonicum*, and all plants of F_2 and later generations up to F_6 were the same colour. The second case was first noticed by Caporn (1918) in a cross between *polonicum* and *durum*, and was studied in detail by Engledow (1920, 1923), who termed the phenomenon "shift." It was found that, although the long glume of *polonicum* and the short glume of *durum* gave a simple 1 : 2 : 1 ratio, the extracted pure long forms were far shorter than the original long parent. Shift was also noticed by Vavilov and Jakushkina (1925) in a *persicum* × *durum* cross. In all these cases the evidence that the parent forms could not be recovered seems to me convincing. Philiptschenko (1927) gives a case, in crosses between *vulgare* varieties, in which, though shift could be detected in F_2, the parent forms were regained in later generations. Since the parent forms were recovered it seems clear that there was no true shift in this case.

Darlington has put forward autosyndesis as an explanation of these phenomena (1928). He suggests that the species concerned being tetraploids, the members of one set of 7 chromosomes in *turgidum*, for example, may be more like the members of the other set in the same species than they are like those of a different species. Thus, if the white chaffed *polonicum* is **WW WW** and the grey chaffed *turgidum* is **ww ww**, F_1 would be **Ww Ww** and allosyndesis would give a 15 : 1 ratio. But with autosyndesis the F_1, which may be written **WW ww**, would only give the gamete **Ww**; so that all plants of F_2 and later generations would have the same formula as the F_1 and, like it, would be white chaffed. In the case of shift in glume length it was supposed that a major factor segregates in the usual fashion, thus giving a 1 : 2 : 1 ratio, but that modifying factors are carried by chromosomes that pair by autosyndesis, so that the parent type would not be recovered.

The explanation is attractive, and should be investigated further.

Malinowski (1926) has advanced a different explanation for shift. On his theory it must be supposed that *polonicum*, AB, differs from *durum*, ab, by two chromosomes A and B which are in some way connected so that they always travel to the same pole. This connection is broken in the F_1 and A becomes attached to b, so that only the gametes Ab and aB are formed. If A controls the major difference in glume

length, and B a small difference only, F_2 will contain Ab with rather shorter glumes than the *polonicum* parent, and aB with longer glumes than the *durum* parent. Actually, of course, A and B need not be two linked chromosomes but might be two linked factors in a single chromosome; a cross-over in F_1 giving Ab, which then remained completely linked instead of AB being linked.

Malinowski has used his hypothesis to explain a number of features of species crosses in wheat. In *Spelta* × *vulgare*, the more evident differences in glume shape and ear density give a 1 : 2 : 1 ratio; and he considers this to mean that the differences were due to a group of completely linked factors. He then found that *vulgare* × *dicoccum* gives new types, which include *Spelta* and *durum*; and concludes that this shows that the factors which were linked in *vulgare* × *Spelta* are no longer linked in *vulgare* × *dicoccum*, though this does not seem to me necessarily to follow. For various reasons he was unable to regard this linkage as ordinary linkage, and proposed the hypothesis of linkage between chromosomes, for which the following evidence was cited:

(1) The appearance of new types when hexaploids and tetraploids are crossed; *e.g. vulgare* × *dicoccum* giving *Spelta* and *durum*; *polonicum* × *vulgare* giving *dicoccum*, *durum* and *Spelta*. In these crosses Malinowski considers that the reason why the linkage between chromosomes is broken is the existence of univalents in the F_1.

(2) In crosses such as *vulgare* × *dicoccum* the parent *dicoccum* is regained more often than the parent *vulgare*.

(3) In the same crosses the parent types are regained only in small numbers.

(4) Shift and the other cases dealt with above.

The phenomenon studied in (1) to (3) was the inheritance of type, as determined by "the sizes and shapes of glumes and spikelets"; (2) is clearly a consequence of the association between type and chromosome number coupled with the fact that chromosome loss and other factors (p. 226) cause a preponderance of forms with low numbers; while (3) occurs because many plants have an intermediate number in F_2, and for other reasons dealt with above (pp. 231–9). For (1) a different explanation, involving the effect of the additional chromosomes of the hexaploid species on type, has been offered (Watkins, 1928).

In this explanation the parent *vulgare* and *Spelta* forms are supposed to have the haploid formulae $\mathbf{kK'}$ and $\mathbf{K_sK'}$, and *dicoccum* the formula $\mathbf{K_s}$; $\mathbf{K'}$ being carried by the extra chromosomes of the hexaploid. The cross *vulgare* × *dicoccum*, $\mathbf{kK'} \times \mathbf{K_s}$, would give the new types $\mathbf{K_sK'}$ and $\mathbf{k}$;

of which the former is the *Spelta* type and the latter a new type not described by Malinowski but mentioned by Kajanus (1923 *a*, *b*). The regular appearance of new types in most crosses between tetraploid and hexaploid wheats was explained in this way, and the residue are likely to yield themselves to further investigation. In my opinion the facts cited by Malinowski in support of his very ingenious hypothesis are better explained in the various ways suggested above.

(7) CUMULATIVE FACTORS.

The cumulative factor theory was first advanced by Nilsson-Ehle (1909, 1911) from his work on wheat and oats. In wheat he showed that red chaff colour might be due to 1 or to 2 factors, and that red grain colour might be caused by 1, 2 or 3. Now that it is known that *T. vulgare* is a hexaploid species, several writers have argued that it probably contains three similar sets of 7 chromosomes in its gametes, and that many of its characters should therefore depend on 3 factors. The suggestion is in some ways attractive. It is a logical conclusion; it may explain why so many characters show an almost continuous range of variation and why it is that the inheritance of so few wheat characters has been put on a factorial basis. Undoubtedly, a careful comparison of variation within the diploid, tetraploid and hexaploid groups should be made for several characters; and the possibility that the results could be explained by 1, 2 or 3 factors, respectively, should be tested genetically. No doubt difficulties would arise, especially since it is not known how far the so-called cumulative factors are really additive in their effects. Nilsson-Ehle himself pointed out that races that gave a 15 : 1 ratio for chaff colour were of a deep red, but that some races which gave a 3 : 1 ratio might be just as deep in colour, and only the splitting numbers could show whether a 1 or 2 factor race had been used.

It is rather surprising that, except for a note by Castle (1928), to which my attention has recently been drawn, one important implication of the view given above seems to have been overlooked. When cumulative factors were first discovered Nilsson-Ehle suggested that they might form the basis of the inheritance of the so-called quantitative characters, which appear to give a continuous range of variation in F_2. This view has been widely accepted; but, if the above reasoning be correct, *T. vulgare* is a special case—a polyploid species in which cumulative factors are to be expected—and cannot be used as support for a general theory of the inheritance of size. Lindstrom (1926, 1928) has given strong experimental evidence for the existence of single factors that control size; but,

if we except the case of wheat, the evidence for cumulative factors is far less satisfactory. The method given by Philiptschenko (1926, 1928 *a*, *b*) for testing the number of factors involved in different crosses may give useful results, but has not yet been adequately tested. To accept the cumulative factor theory of size inheritance on the evidence now available is not warranted in my opinion, and may mean that important phenomena are being overlooked.

CONCLUSION.

There is no doubt that hybridisation is the most plausible explanation for the origin of the tetraploid and hexaploid wheats. The three groups are clearly separated by their morphology, geographical distribution and chromosome number. The two known methods by which tetraploids can arise are simple chromosome doubling, as in the autopolyploid *Primula sinensis*, and hybridisation followed by doubling, as in the allopolyploid *P. kewensis*. The second method is evidently more probable for the tetraploid wheats, since it would explain at once, without further assumptions, why there is no tetraploid like a diploid, and why the tetraploids vary about types widely different from the diploids. Furthermore, hybridisation gives an immediate explanation for the origin of the new characters, and for the greatly increased variability, which distinguish the former group so clearly from the latter. Our only assumption is an unknown species with which one of the diploids has crossed. The change from tetraploid to hexaploid is distinguished by exactly the same features; and again, therefore, agrees with the theory of a hybrid origin. There are difficulties, however. Thus, the 14 chromosome wheats apparently do not occur in Northern Africa, where the tetraploids are supposed to have originated; nor does chromosome pairing in the hybrids between the two series appear to be as regular as might have been expected.

Percival has given evidence that the hexaploids came from a cross between a tetraploid wheat and *Aegilops ovata* or *A. cylindrica*. Chromosome doubling after such a cross would give, however, 56 chromosomes instead of 42; and the evidence of hybrid cytology, while suggesting that there may be some relation between *T. vulgare* and *A. cylindrica*, does not agree with the view that the former arose in the way suggested. Related genera, such as *Aegilops*, must evidently be considered in connection with evolution in *Triticum*; but since polyploid series exist in *Aegilops* as well, and these may have had a hybrid origin, we must admit the possibility that many of the species in the genera *Aegilops*,

Secale, *Agropyrum* and *Triticum* are in some confused fashion related. The origin of any of these species is not likely to be an easy problem; but something may be learned from the hybrids between the different forms, and if a synthesis of *T. vulgare* or some other form is ever effected it will certainly help the solution of several of the problems discussed in this paper.

With regard to the further evolution of the wheat forms we can but indicate briefly the more obvious considerations. The tetraploid group contains a wide range of forms in which the varying characters occur in most of the possible combinations. Character recombination would follow from natural crossing; but we have also to explain why the different forms, instead of being all equally frequent, are grouped into so-called species connected by transition forms. No doubt agricultural conditions would have some effect; *durum* and *turgidum*, for example, would normally be grown under different conditions and their intercourse thereby restricted. In other cases there may be genetical reasons; thus *T. polonicum* owes its specific rank to a genetical association between a number of characters. Time may be another factor. If natural crossing between two widely different types, *A* and *B*, were not too frequent it would give, after a moderate interval, two polymorphic species connected by transition forms.

Next, we have to consider how the original variations occurred; *e.g.* the origin of black, red, or white chaff, long or short awns, and so on. One possibility is loss mutation. Although it is doubtful whether any certain case has been observed in wheat, there is indirect evidence in the existence of *polonicum* with short grains and *durum* with long grains, despite the apparently complete linkage between these characters. Secondly, whatever may be the mechanism by which speltoid mutants arise, the same phenomenon may occur in tetraploids, and might be important since the change involves a number of factors, *A* giving a markedly different form than *B*. If *B* produced further types, *e.g.* by loss mutation, we should have a small group of forms deserving the term species as much as some of the existing species deserve it. Finally, two or more different species, *e.g. dicoccoides*, *dicoccum*, *durum* and *persicum*, may have arisen directly from the diploids by hybridisation; and the whole range of variation might have been comprised in these few primitive forms. *Dicoccum* appears to be the most primitive cultivated wheat in the series, and the sudden appearance of *durum* is perhaps more easily explained by a separate origin than by origin from *dicoccum*; and new characters, one of the arguments for a hybrid origin for the tetra-

ploid wheats, are far more numerous in *durum* and related species than in the primitive *dicoccum*. Several separate origins would also explain the grouping into species; diversity within the species, and transition forms, having come in the various ways suggested above.

The importance of the factors we have discussed cannot be estimated until we know exactly how the different characters vary, how they are combined, and how common the different combinations are. In addition, adequate genetical knowledge is necessary.

Nor must it be forgotten that evolution in diploids is little understood, and that whatever factors operate in them presumably operate in polyploids as well, perhaps in a more complicated fashion. This would diminish the chance that the existing polyploids can be synthesised from existing diploids.

In the hexaploid series the situation is similar. The species *Spelta*, *compactum* and *sphaerococcum*, are all closely related to *vulgare*; and although the latter is very polymorphic it does not fall into clearly defined groups. One of the arguments that these wheats had a hybrid origin is that beardless, and several other characters, appear in them for the first time. Pushed to its conclusion this argument implies at least two separate origins for *vulgare* since there are two types of beardless, caused by different factors (Howard and Howard, 1912, 1915). This demands frequent hybridisation between widely separated species, and Popova (1923) actually found in Turkestan great numbers of hybrids of *T. vulgare* with *A. cylindrica* Host. and *A. crassa* Boiss.

Except for Winge's theory of the origin of polyploids, genetics and cytology have not, so far, taught us very much about the origin of the wheat species or their subsequent evolution. Something may be learned from the cytology of their hybrids with related genera; but so far this work has not been extensive, and must be done in greater detail if affinities are to be deduced from chromosome pairing. Within the genus itself work on species crosses has been devoted, naturally enough, chiefly to special problems such as sterility; but since the principles of inheritance in these crosses have now been worked out in a preliminary fashion, and a factorial analysis can be made, some progress should be possible.

Similarity between the 7 chromosomes of the diploid wheats and 7 from the tetraploids, and again between the 14 of the latter and 14 from the hexaploids, was suggested by the results of hybrid cytology. Further development of the polyploid theory—that every set of 7 is more or less similar to every other set—is due especially to Winge (p. 240). If the

theory of hybrid origin be accepted, we must regard *T. vulgare*, for example, as being composed of three sets of chromosomes A_1, A_2 and A_3; the chromosomes of A_1 being more or less similar to those of A_2 and A_3, according to the difference between the species that originally entered the cross and to the extent of subsequent changes. The genetics of the pentaploid hybrids gives direct evidence in favour of this view since it has been shown that the unpaired chromosomes from the hexaploid parent do, in some cases, carry factors similar to those carried by the paired chromosomes. Apart from this the only evidence we have is the existence of cumulative factors. However, an explanation based on the polyploid theory has been suggested for the origin of speltoid mutants; and, subsequently, for the irregular inheritance sometimes observed in crosses between the tetraploid wheats. As developments from the polyploid theory both explanations are attractive; but it must be admitted that the former does not, in its present form, completely explain the facts, and that the latter so far lacks experimental confirmation.

Similarly, the polyploid theory agrees with the general facts of systematics, though here again experimental proof is lacking. In diploids, if a character is affected by a factor A_1 only two forms occur, namely those with the gametic formulae a_1 and A_1. In tetraploids and hexaploids the number of possible variants would be greatly increased, and we can understand the reason for "the extraordinary complexity and almost endless number of varieties and intermediate forms of the *vulgare* race" noted by Percival (see p. 197). Moreover, if A_1, A_2 and A_3 are different, we can have in the hexaploid a series of forms such as $A_1A_2A_3$ which are not possible in the other series; and we can understand why differences between the groups are more often differences in degree than in kind.

There are clearly good grounds for supposing that many features of the genus are the outcome of its polyploid nature, but so far there is little experimental proof.

I wish to record my indebtedness to Prof. Sir Rowland Biffen, who has always placed his wide knowledge of wheat at my disposal; and to Prof. Percival for his frequent kindness in showing me his wheat collection.

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ON THE SERIES OF ALLELOMORPHS CONNECTED WITH THE PRODUCTION OF BLACK PIGMENT IN RABBITS.

By R. C. PUNNETT, F.R.S.

Introduction.

Some years ago (1912) I showed that there existed a black form of the rabbit which behaved as dominant to agouti, whereas the normal black in this species is a recessive. I suggested that this was due to a dominant factor, **D**, which inhibited the action of the agouti factor, **A**, and that this factor was completely (or almost completely) linked with the factor for extended pigmentation (**E**) such as occurs in normal blacks and agoutis, as opposed to that for restricted pigmentation (**e**) found in tortoises and yellows.

With the advent of the conception of multiple allelomorphs Wilson (1913) suggested that the simplest way of regarding this case was to suppose that dominant black, normal black, and tortoise depended upon three allelomorphs, and that in the presence of the agouti factor (**A**) the series became black, agouti, and yellow.

More recently independent experiments by Castle and by myself (1924) showed that the factor (**J**) for the mixed yellow and black coat pattern of the Japanese rabbit must be regarded as allelomorphic to black (**E**) and tortoise (**e**). In the present paper evidence is brought forward in favour of the factor for dominant black (**D**) also being allelomorphic to Japanese, as indeed was to be expected.

Some years ago Onslow (1922) worked out the genetics of the "steel" rabbit, a dark agouti form with the belly pigmented instead of white as in the ordinary agouti. He showed that steel is a heterozygous form, and that, in material homozygous for **A**, steel × steel gave blacks, steels and agoutis in the ratio 1 : 2 : 1. As Onslow pointed out, the simplest explanation is to suppose that here again we are concerned with a factor for dominant black (**D′**), allelomorphic to that for normal recessive black (**E**). In the presence of **A** the **D′D′** rabbit is black, the **D′E** is steel, and the **EE** rabbit is agouti. At present we may regard the "steel" factor (**D′**) as distinct from the dominant black factor (**D**), for reasons which will appear later.

Hitherto **D′** has not been related to any member of the multiple allelomorphic series **D, E, J, e**, except to **E**. The object of the following

experiments was to test the relations of **J** to **D** and **D′**, in the light of Castle's work and my own with the Japanese rabbit.

MATERIAL.

I had long since ceased to breed dominant blacks, but I was fortunate in being able to procure from my friend, Mr T. H. Riches, a buck descended from my original material. He turned out to be **DDaa**, and also heterozygous for blue and for the Himalayan pattern.

For my "steel" material I am indebted to the Hon. Mrs Onslow, who kindly sent me a pair when her husband's rabbits were dispersed after his death. Unfortunately they proved to be sterile with one another, and very shy breeders with other stock. The **D′** material used was extracted from crosses derived from the original steel buck.

For the work I had in mind I should have liked to use **DDAA** and **D′D′AA** animals, but to have built up strains of the above constitutions in a reasonable time was not possible with the limited accommodation available. For this reason the experiments are more numerous and less orderly than I could have wished. To set them all out would be tedious and I shall, therefore, give selected evidence only. But it should be stated that the various miscellaneous data accumulated are in accordance with the interpretation given in terms of a series of multiple allelomorphs.

THE RELATION OF D TO J.

The buck obtained from Mr Riches (♂ 144) was mated with a Japanese doe (♀ 138) of the constitution **AaJJ**, and gave eight blacks. Of these four ♀♀ and one ♂ were used to produce the F_2 generation set out in Table I.

TABLE I.

	Black	Blue	Chocolate	Lilac	Himalayans	Japanese
♀ 170 × ♂ 169	10	—	—	—	—	7
♀ 171 × „	6	—	4	1	4	2
♀ 172 × „	6	1	1	1	5	2
♀ 173 × „	3	—	2	—	1	2
	25	1	7	2	10	13
	$\underbrace{}_{35}$					

The appearance of blues and Himalayans is due to ♂ 144, which was known from other evidence to have carried these characters, while the chocolate came into the cross through ♀ 138. The Himalayans were killed early before it could be decided whether they corresponded to the

self-coloured or to the Japanese type. Of the rest there were thirty-five self-coloured and thirteen Japanese, a fair approximation to the 3 : 1 ratio expected on the assumption that **D** and **J** are allelomorphic. Further, although some of the F_1 animals probably carried **A**, no agouti-marked animal appeared in F_2. This also is in accordance with expectation on the assumptions that **D** and **J** are allelomorphic, and that the **DJA** animal shows no agouti ticking. Evidence for the latter assumption will be given below (cf. p. 272).

Twelve of the F_2 blacks were then crossed with Japanese, nearly all of which were homozygous for black (**BB**). The results of these matings are set out in Table II.

TABLE II.

F_2 black		Japanese		Black	Chocolate	Japanese
♂ 211	×	♀ 188	gave	2	—	2
♂ 212	×	♀ 166, ♀ B 11	,,	8	—	—
♀ 228	×	♂ 227	,,	4	—	—
♂ 229	×	♀ 215, ♀ B 12	,,	5	—	10
♀ 234	×	♂ 163	,,	2	—	3
♀ 235	×	♂ 165	,,	2	—	5
♀ 236	×	♂ 187	,,	6	—	1
♀ 237	×	♂ 187	,,	10	—	—
♀ 238	×	♂ 227	,,	5	—	—
♀ B 2	×	♂ 227, ♂ 187	,,	10	—	—
♂ B 3	×	♀ 217	,,	1	1	1

Of the twelve animals tested four, viz. ♂ 212, ♀ 237, ♀ B 1 and ♀ B 2 were evidently homozygous for **D**; six, viz. ♂ 211, ♂ 229, ♀ 234, ♀ 235, ♀ 236 and ♂ B 3 were heterozygous; while ♀ 228 and ♀ 238 were not sufficiently tested for certainty. The six definite heterozygotes gave in all nineteen self-coloured and twenty-two Japanese, a near approach to the equality expected on the assumption that **D** and **J** are allelomorphic.

Of the Japanese rabbits used one, ♂ 187, was known from other evidence to have been heterozygous for **A**. With ♀♀ 236, 237, and B 1 he gave twenty-nine self-blacks, none of which had any trace of agouti ticking. Since about 50 per cent. of these animals must have carried **A**, it is clear that the **DJA** rabbit is a full black in appearance. In this respect the factor for Japanese (**J**) behaves similarly to that for tortoise (**e**) (cf. Punnett, 1912).

These experiments are consistent with the view that **D** and **J** are allelomorphic.

THE RELATION OF **D′** TO **J**.

As already stated the **D′** factor was derived from one of Onslow's steels, viz. ♂ 137. Mated with a yellow doe (♀ 119) he gave agouti-blacks[1] and agoutis. Of these an agouti-black doe (♀ 178) and an agouti buck (♂ 176) were bred together and gave in all:

$$\left.\begin{array}{l}\text{2 agouti, 1 black, 3 steel, 1 agouti-black}\\ \text{1 cinnamon, 1 chocolate, 1 chocolate steel, 1 dark chocolate agouti}\end{array}\right\}\text{ 5 yellow or orange,}$$

where expectation, on the assumption that **D′**, **E** and **e** are allelomorphic, would be

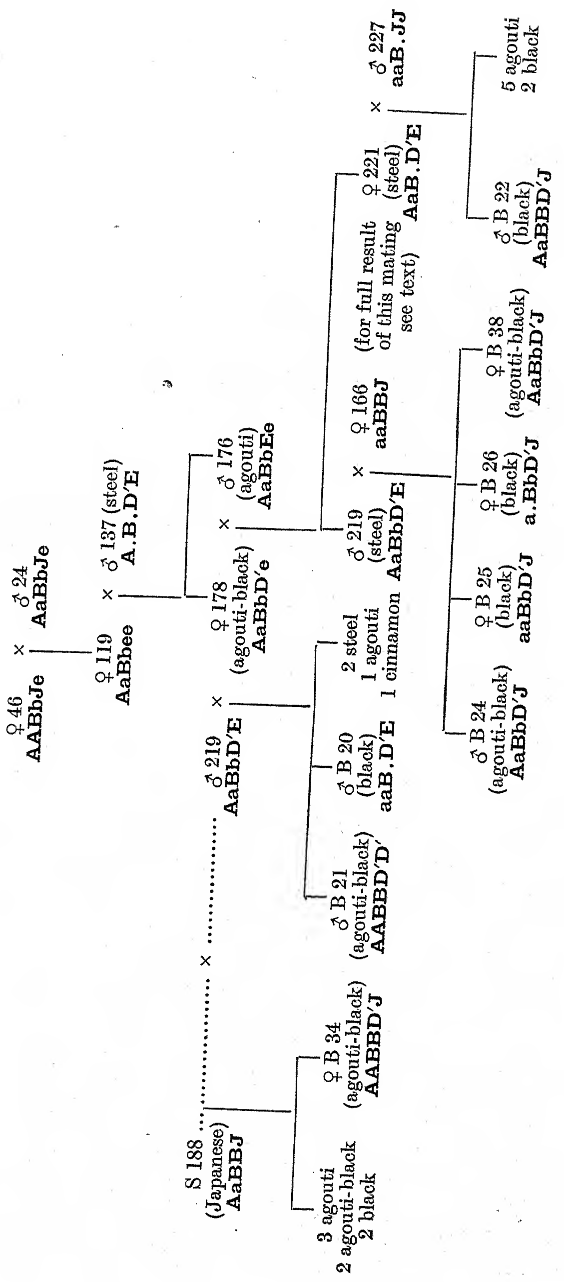
$$\left.\begin{array}{l}\text{2·25 agouti, 2·25 black, 2·25 steel, 2·25 agouti-black}\\ \text{0·75 cinnamon, 0·75 chocolate, 0·75 steel, 0·75 dark chocolate agouti}\end{array}\right\}\text{ 4 yellow or orange.}$$

It is remarkable that, even in the small number bred, all of the expected classes appeared, and closely in the proportion expected. As shown in Pedigree I (p. 269), two of the steels, viz. ♂ 219 and ♀ 221, were subsequently used for breeding purposes, and a certain number of the animals bred were analysed by means of various matings. The results throughout were found to be consistent with the view that **D′**, **E**, **J** and **e** behave as multiple allelomorphs.

One further experiment may be referred to in more detail. From Pedigree I it will be seen that ♂ 219 was mated with a Japanese doe (♀ 188) with whom he gave three agoutis, three agouti-blacks and two blacks. One of the agouti-blacks, ♀ B 34, was tested and found to be **AABBD′J** in constitution. She was then mated with ♂ B 48, a black of the constitution **aaBBEE**. With him she gave eleven agoutis and eight steels. On the assumption that **D′**, **E** and **J** are allelomorphic these agoutis should all be **AaBBEJ**, and the steels all **AaBBD′E** in constitution. The agoutis bred together should give agoutis, blacks and Japanese in the ratio 9 : 3 : 4. Actually two does (♀ B 108 and ♀ B 110) mated to the same buck (♂ B 112) gave seven agouti, three blacks and two Japanese. Again, the steels bred together should give agoutis, blacks, and steels in the ratio 3 : 7 : 6. Actually two does (♀ B 109 and ♀ B 111) mated to the same buck (♂ B 114) gave five agoutis, nine blacks, and six steels. In either case the results, both qualitative and quantitative, are in full agreement with the assumption that **D′**, **E**, and **J** are members of the same allelomorphic series.

[1] *I.e.* blacks with a small but variable amount of agouti ticking. The variety is figured in Vol. II, Pl. XII, fig. 2, of this *Journal*.

PEDIGREE I.


♀ 46 AABbJe
♂ 24 AaBbJe
♀ 119 AaBbee
♂ 137 (steel) A.B.D′E
♀ 178 (agouti-black) AaBbD′e
♂ 176 (agouti) AaBbEe
♂ 219 (steel) AaBbD′E
♀ 166 aaBBJ
(for full result of this mating see text)
♀ 221 (steel) AaB.D′E
♂ 227 aaB.JJ
♂ B 22 (black) AaBBD′J
5 agouti
2 black
♂ B 24 (agouti-black) AaBbD′J
♀ B 25 (black) aaBbD′J
♀ B 26 (black) a.BbD′J
♀ B 38 (agouti-black) AaBbD′J
S 188 (Japanese) AaBBJ
♂ 219 AaBbD′E
♀ B 34 (agouti-black) AABBD′J
3 agouti
2 agouti-black
2 black
♂ B 21 (agouti-black) AABBD′D′
♂ B 20 (black) aaB.D′E
2 steel
1 agouti
1 cinnamon

THE RELATION OF **D** TO **D′**.

To test the relation of **D** to **D′**, the steel buck (♂ 219) mentioned above (p. 268) was mated with two extracted dominant black does (♀ B 1 and ♀ B 2) both of the constitution **aaBbDD** (cf. p. 267). Since ♂ 219 was genetically **AaBbD′E**, the expectation from this type of mating is as follows:

ABD′ **aBD**	**ABE** **aBD**	**AbD′** **aBD**	**AbE** **aBD**	**aBD′** **aBD**	**aBE** **aBD**	**abD′** **aBD**	**abE** **aBD**
Black	Agouti-black	Black	Steel	Black	Black	Black	Black
ABD′ **abD**	**ABE** **abD**	**AbD′** **abD**	**AbE** **abD**	**aBD′** **abD**	**aBE** **abD**	**abD′** **abD**	**abE** **abD**
Black	Steel	Chocolate	Chocolate Steel	Black	Black	Chocolate	Chocolate

This expectation is based upon the known facts (1) that the **DE** animal carrying **A** is agouti-black, (2) that the corresponding chocolate class is chocolate steel, and (3) that the **DE** animal containing **A** and also heterozygous for chocolate (**Bb**) is steel in appearance (cf. Punnett, 1912). It is also based on the assumption that the **DD′** animal carrying **A** is, like the **DD** animal, full black. Evidence in support of this assumption is given later (p. 271).

From this cross then five colour classes are expected, though two of them, the agouti-black and the chocolate steel, are rare, occurring only once in sixteen times. Actually four of the classes appeared among the twenty animals bred, the rare agouti-black class alone being unrepresented. On the other hand there were two of the corresponding chocolate class. The actual and expected figures are as follows:

	Black	Steel	Chocolate	Agouti-black	Chocolate steel
Actual	10	4	4	—	2
Expected	11·25	2·5	3·75	1·25	1·25

The correspondence between the expected and the actual result is sufficiently close in view of the small numbers bred.

A point of interest is that such steel rabbits as occur from this mating should be genetically **AaBbDE** in spite of the fact that the "steel" factor **D′** enters into the mating. The chocolate steels should also be **DE** in constitution. One of the steels (♀ B 16) and one of the chocolate steels (♀ B 39) were tested and were both found to be **DE** as expected.

Of the blacks three were tested and constitutionally determined as follows:

♀ B 17 was **AaB.DD′** (she might have been **BB** or **Bb**),
♀ B 18 „ **aaBBDE**,
♂ B 19 „ **AaBBDD′**.

The analysis of ♀ B 17 and ♂ B 19 proved the correctness of the assumption that the **DD′A** animal is a full black (cf. p. 270).

♂ B 19 was also mated with a black doe (♀ B 68) of the constitution **aaBBEE**. He produced two blacks, three agouti-blacks and one steel, these three classes only being expected in the ratio 2 : 1 : 1.

The above facts are all consistent with the view that **D** and **D′** segregate from one another, and are both members of the series of allelomorphs in which the five terms **D, D′, E, J,** and **e** have been hitherto identified.

GENERAL REMARKS.

A point of some interest in connection with this series of allelomorphs is the phenotypical expression of some of the heterozygous forms when **A** is present as an indicator. The earlier experiments on the **D** black showed that the **DD** form was always full black, the **DE** form agouti-black, and the **De** form again full black. This is true for **BB** animals. When heterozygous for chocolate (**Bb**) the **DE** form is dark steel, whereas the other two remain full black. These later experiments have confirmed the earlier results and have provided the additional information that the full black of the **DD′** and the **DJ** combinations is not affected by the presence of **A**. Koller (1930) recently showed that the formation of **E** black can be inhibited by **A** *in vitro*, whereas that of **D** black is not inhibited. Since the **DEA** rabbit is agouti-black we must suppose that **A** can produce a slight inhibitory effect on this combination. The **DJA** combination has always proved to be full black, nor is this surprising in view of the fact that the Japanese rabbit carrying **A** has never been found to show any trace of agouti marking (Punnett, 1924). **J** black, like **D** black, is what we may term a "refractory" black. Now since the **DeA** combination has always been found to be full black it would seem natural to regard the black pigment of the tortoise rabbit (**e**) as being also refractory in nature, and hence qualitatively different to **E** black to which it behaves as a simple recessive. But this view is negatived by the fact that the **eeA** rabbit is a yellow, with definite agouti ticking in spite of the paucity of black pigment, and with a white belly. We are driven to suppose that the **e** black, like the **E** black, is non-refractory. Why then should the **DEA** form, which contains two "full" colour factors, show some agouti ticking, while the **DeA** form, containing a "full" and a "dilute" one, is completely black?

Although what follows is admittedly crude speculation it is possible to look at the matter in the following way. The **DD** rabbit, with completely refractory black pigment, is always full black when **A** is present; and if it were possible to get a **DO** animal we should expect this also to be full black. The **DE** animal possesses the means of producing both refractory and non-refractory pigment, and the production of a certain amount of the latter enables **A** to bring about the formation of an agouti-black. When the **DE** animal is heterozygous for chocolate (**b**) the ticking is accentuated because chocolate is more readily inhibited than black[1]. The **De** animal also possesses the means of producing both refractory and non-refractory pigment, but the power of producing the latter is here very much less than in the case of the **DE** animal. The power of producing refractory pigment, however, is presumably just as great, and it seems not unlikely that the full black of the **DeA** animal may be due to the almost exclusive formation of the refractory **D** pigment, which is possible in competition with **e** but not in competition with **E**.

We may now turn to similar considerations in connection with **D′**. Generally speaking **D′** may be regarded as a refractory black, but less refractory than **D**. The **D′D′A** animal is generally full black, but sometimes it shows traces of agouti marking even when homozygous for **B**[2]. The **D′EA** animal is the "steel" of the fancy, and corresponds with the agouti-black in the **D** series. I have unfortunately no evidence as to whether the agouti markings are more pronounced when the animal carries chocolate. The **D′eA** rabbit in my experience is generally agouti-black, and indistinguishable in appearance from the **DEA** rabbit[3]. In some cases, however, rabbits which must have been of this constitution were recorded as full black before killing at a few weeks old. The ticking often does not develop until later, and it is possible that these rabbits might have become agouti-black. Whether **D′eA** rabbits can be full black when adult is at present undecided.

The **D′JA** animal may be either full black or agouti-black, and the

[1] This statement rests upon the observed facts (1) that the cinnamon (= chocolate agouti) is relatively less pigmented than the corresponding black agouti, and (2) that the chocolate steel, **AAbbDE**, is more obviously agouti marked than is agouti-black, **AABBDE**, its corresponding term in the black series.

[2] This was the case in ♂ B 21, cf. p. 269.

[3] In 1918, when in the Isle of Wight, I came across a litter which contained agouti-blacks, agoutis, and yellows. At that time the **DEA** rabbit was the only form of agouti-black with which I was acquainted. I purchased one of the agouti-black does and mated her to a tortoise ♂. She gave agouti-blacks, agoutis, yellows and tortoises, and must have been **AaD′e** genetically.

amount of ticking may vary from a trace to that characteristic of the normal agouti-black. I have hitherto been unable to relate these differences with any feature in the genetical constitution. They do not depend upon the animal being heterozygous for chocolate, since ♂ B 21 (**AABBD′D′**) with a yellow doe (♀ 220) gave seven young, all agouti-blacks. Since ♀ 220 was heterozygous for chocolate presumably some of the young were **BB** and others **Bb**. With a Japanese doe (♀ B 8) ♂ B 21 produced eleven young, also all agouti-blacks, *i.e.* the **D′JA** and the **D′eA** young from this buck were all similar in appearance.

Apart, therefore, from a certain amount of minor variation the reactions of **D′** in its combinations with **E**, **J**, and **e** are along similar lines to those of **D**, and such as might be expected if the chief difference between them lies in the fact that one is more refractory to the inhibitory activity of **A** than is the other.

Lastly, there is one further point which calls for brief mention, although its bearing is by no means clear. The ordinary agouti rabbit which carries **J**, viz. the **EJA** rabbit, frequently shows smudges of black which may occur on almost any part, including the light belly (cf. Punnett, 1924). On such heterozygotes the refractory Japanese black appears to be distributed independently of the **E** black, as indeed we know it to be in the **eJA** type. But although I have examined some dozens of agouti-blacks of the **D′JA** kind I have never been able to detect any irregularity in the distribution of the agouti ticking. In other words the **J** black does not give the appearance of being superimposed on the **D′** black as on the **E** and **e** blacks. It is tempting to suppose that **D′** is chemically more akin to **J** than are **E** and **e**, so that the combination **D′J** gives rise to a fairly uniform pigment; whereas, in the combinations **EJ** and **eJ**, **J** always acts independently of **E** and **e**. In any case this series of allelomorphs is one of the most interesting hitherto met with, and it is hoped that further light may eventually be thrown upon it by other experiments now in progress.

SUMMARY.

Earlier work had shown that of the factors connected with the production of melanic pigment in the rabbit two groups of three each, viz. **D**, **E**, **e**, and **J**, **E**, **e**, behaved as though in either case the three factors were allelomorphic. Evidence is now adduced to show that **D** and **J** are allelomorphic, and further evidence is brought forward to show that **D′**, the "steel" factor, also belongs to the same series of allelomorphs. The five members of the series differ in their reactions towards the inhibitory

agouti factor (**A**), **D** and **J** being completely refractory, **E** and **e** being non-refractory, and **D′** partially so. Various points are discussed in connection with the phenotypical manifestation of various combinations of the five allelomorphs.

I wish to acknowledge my indebtedness to the Government Grant Committee of the Royal Society, without whose assistance these experiments could not have been undertaken.

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GENETIC AND DISTRIBUTIONAL STUDIES OF THREE SUB-SPECIES OF *PEROMYSCUS*[1].

By FRANCIS B. SUMNER.

(With Plates VIII–XI, Twenty-seven Text-figures and Six Tables.)

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[1] These studies were conducted at the Scripps Institution of Oceanography at La Jolla, California, largely with the aid of a liberal grant from the Carnegie Institution of Washington.

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I. Introduction.

Intensive field studies of various groups of animals, both vertebrate and invertebrate, are making it increasingly evident that the phenomenon of geographic variation within a species, or a group of closely related species, is one of very wide occurrence[1]. Among students familiar with the facts of the case the belief is now probably fairly general that the differentiation of these geographic races or sub-species represents one of the most important ways in which the divergence of organic groups commences. It is consequently surprising, in view of the abundance of some of this material and of the absence of insurmountable technical difficulties in rearing it, that so few geneticists have directly attacked the problem of the inheritance of sub-specific characters. Preoccupation with the simpler, more sharply defined problems of Mendelian inheritance is doubtless responsible in large degree for this attitude. The view is often expressed that the phenomena manifested in specific and sub-specific crosses are too complicated for profitable investigation at present, since the characters involved do not seem to admit of "critical" Mendelian analysis.

It is doubtless true that they do not admit of critical analysis, according to prevailing Mendelian standards, and this fact is certainly an important limitation to the scope of studies conducted with such material. Perhaps it will always remain so. But the question arises whether much of first-rate importance cannot be learned from such studies, despite these handicaps, and whether all knowledge of the genetics of sub-specific differences must await the time when we can resolve them into a definite number of nameable genes, each assigned to its proper linkage group.

It would seem, for example, quite relevant to genetics to decide such questions as the following: whether sub-specific differences are inheritable at all; whether they are subject to appreciable modifications by external influences; whether and to what extent individual variations in these same characters, within a sub-species, are inheritable; to what extent the various characters which differentiate one sub-species

[1] A valuable general discussion of this subject has been recently prepared by Rensch (1929).

from another are found to be correlated, (1) in dealing with a group of closely related sub-species, and (2) within the limits of a single sub-species; whether the correlation, if it exists, appears to be explainable by the linkage of genetic factors, or by the dependence of the characters in question upon common genetic factors, or by some other cause; whether there is any tendency toward dominance or recessiveness of sub-specific characters in crosses, and whether the aggregate characters of one of the sub-species tend to behave as a unit in this respect; whether there is any evidence of genetic segregation in the F_2 generation of sub-specific hybrids, in back-crosses, etc., and if so whether the character differences in question depend upon single genetic factors, or upon multiple factors; whether, in the latter event, the number of principal factors concerned may be approximately estimated; whether there is any tendency, in these generations, for the several characters which distinguish one sub-species from the other to segregate together, thus increasing any correlations which may previously have been exhibited; finally, whether there is any evidence that sub-specific characters may blend, as a result of crossing, in such a way as to be irrecoverable in later generations.

The foregoing list of questions could be greatly extended. None of them depend for their answers upon "critical analysis" of the usual Mendelian type. To what extent the *Peromyscus* studies of the past fifteen years have contributed to their solution I must leave others to judge. But that studies of the sort here indicated have been urgently called for is evident from the fact that when the present investigations were commenced zoologists were still seriously discussing whether the differences between geographic races of birds and mammals were hereditary at all. So far as I have been able to learn, no real experimental test of this question had previously been made with either of these groups.

The experiments to be discussed in the following pages form part of a rather extended programme which has been conducted by the author and his co-workers since 1914. The results have been reported in numerous papers throughout this period[1].

It has been inevitable that my point of view respecting some of the

[1] The chief of these, so far as they bear on genetic or distributional problems, are as follows (those most relevant to the present discussion being italicised): Sumner, 1915, 1917, 1917 *a*, *1918*, *1918 a*, *1918 b*, *1920*, *1922*, *1923*, *1923 a*, 1923 *b*, 1924, *1924 a*, 1924 *b*, 1925, *1926*, *1927*, *1928*, 1928 *a*, *1929*, *1929 a*, 1929 *b*; Sumner and Collins, 1922; Sumner and Huestis, 1921, *1925*; Sumner and Swarth, 1924; Collins, 1923; Huestis, *1925*.

theoretical questions involved should undergo considerable change with increasing knowledge of the facts. Thus, for some years, I was disposed to share the view of many taxonomists and others that the characters which distinguish species, sub-species and other "natural" groups belong to a quite different category from the characters which distinguish the various "artificial" races and "mutant" types that have been used in most Mendelian experiments[1]. The obvious differences between these two types of variation, both in their incidence and in their mode of inheritance, cannot be disputed. I am nevertheless now disposed to accept as probable the interpretation which has been given to these differences by most recent geneticists, namely, that they are due largely to differences in the number of genetic factors which are involved in the two cases.

My own change of view-point on this subject has resulted mainly from two considerations: (1) Convincing evidence of genetic segregation, in respect to various colour characters, has been revealed in the course of the *Peromyscus* studies. This was not obvious in the earlier hybridisation experiments which were undertaken (Sumner, 1920), but became increasingly evident with more extended experiments and more thoroughgoing analysis (Huestis, 1925; Sumner and Huestis, 1925), and has been shown most strikingly of all in the series discussed in the present paper. (2) Certain variations of the "mutant" type, occurring sporadically within a species, have been found to be inherited with much the same appearance of imperfect segregation as are the differences between our "natural" species and races. In Mendelian terms, they seem to depend upon a number of partially dominant factors of varying potency. Thus the sharp distinction between one type of inheritance and the other seems to fall away (Sumner, 1928).

The remarks in the last few paragraphs must not be construed, however, as a claim (or admission) that the "multiple factor" interpretation of all specific and sub-specific characters yet rests upon a firm foundation. All that is claimed is that the data thus far derived from the study of *Peromyscus* conform fairly well with the requirements of that theory, while there are thus far few data which seem actually inconsistent with it. As has been remarked more than once previously, evidence for genetic segregation is not necessarily evidence for *complete* segregation of the type familiar to us in the case of known Mendelian allelomorphs.

Throughout the entire course of these studies I have been much less

[1] Osborn's (1927) antithesis between "speciation" and "mutation" belongs here.

concerned with the mechanism of hereditary transmission, to which, for the most part, they have little relevance, than with the analysis of racial differences, and the light which these may throw upon the process of evolution. To what extent, if at all, the present studies have contributed to this field will be considered in the closing section of the paper[1].

II. DESCRIPTION OF THE SUB-SPECIES EMPLOYED.

No extended account seems called for here, either of the material or the methods employed in the present experiments. The biometric data regarding the "wild" generation of the parent stocks (*Peromyscus polionotus polionotus*, *P. p. albifrons* and *P. p. leucocephalus*) have been presented in considerable detail in another paper (Sumner, 1926)[2], while the nature of the "characters" here considered, and the means by which they are measured, have been fully discussed in a yet more recent paper (Sumner, 1927).

Briefly, it may be repeated that the species *Peromyscus polionotus* constitutes a group of small, short-tailed mice, occupying portions of the states of Georgia, Alabama and Florida, where it is represented by six recognised sub-species[3]. This grouping may prove, however, to be provisional. *Peromyscus polionotus* appears to be closely related to *P. maniculatus*, the most widely prevalent and geographically diversified member of the genus. Within the species *P. polionotus*, the sub-species *P. p. polionotus* probably represents most nearly the ancestral form. Its range is wider, its habitat more nearly average, and its characters more typical of the genus than those of any other of this group of geographic races. Thus *P. p. polionotus*, viewed dorsally, is of a dark grey-brown colour, not far different from that of many of the other wild mice of various parts of the world. As with most species of *Peromyscus*, the ventral surface of the body, up to a certain level on

[1] It is a pleasure to acknowledge here, as on many previous occasions, the ever-ready help of my colleague, Dr G. F. McEwen, in various matters relating to mathematical procedure.

[2] The figures presented in the present paper do not, in all cases, correspond with those given in the earlier one for a number of reasons. (1) The earlier figures for *albifrons* were based upon material derived from three more or less isolated localities. It will be pointed out below that these local collections exhibited rather wide differences in respect to certain characters. (2) Instead of using the fraction $\frac{R-V}{V}$ as an index of saturation for red, I now use $\frac{R-V}{R}$ $\left(\text{see Sumner, 1927, in which paper, however, this fraction is written } \frac{R-BV}{R}\right)$. (3) Certain values comprised in the earlier table have been omitted from the later one, while a considerable number of new ones have been added in the latter.

[3] Osgood (1909), Howell (1920).

the sides, is of a whitish appearance, due to the lack of pigment in the tips of the hairs covering this region. The basal half or more of each hair exhibits, however, the usual dark pigmentation. A dorsal stripe of dark hairs extends throughout the length of the tail, this contrasting rather sharply with the white hairs which clothe the remainder of the appendage.

The other sub-species which have been described are of a much paler hue, they occupy less typical habitats, and are considerably modified from the supposedly primitive condition shown in *polionotus*. I shall discuss only two of these sub-species. *P. p. albifrons* is found throughout a rather narrow belt, bordering the Gulf of Mexico, and extending, so far as known, from Mobile Bay eastward to Point St Joe, a distance of more than 160 miles. *Albifrons* is a far paler form than *polionotus*, being of a buff or pale brown hue, not far different from that of many of the rodents of our American deserts. The white, ventro-lateral area is considerably more extended than in *polionotus*, while the hairs throughout much of this area are white to their very bases. The dorsal tail stripe is reduced or vestigial. It is narrow and faintly pigmented, and commonly extends only part way from the base to the tip. In some cases it is lacking altogether.

This process of depigmentation has been carried to extraordinary lengths in the case of the third race, *leucocephalus*, which inhabits an island reef, skirting the coast of north-western Florida. This race has a paler coloration and more extensive white areas than any other wild mouse with which I am acquainted, and the tail stripe is entirely lacking.

This island (Santa Rosa Island), as well as the beaches and dunes of much of the adjacent mainland, consist of extremely white quartz sand, covered to only a limited extent by vegetation. One cannot escape the conviction that these conditions have been responsible for the extraordinary modification of the mice which dwell here. That the modification has progressed so much farther in *leucocephalus* than in *albifrons* is doubtless due to the complete isolation of the former throughout a considerable period of time[1].

The three sub-species here considered also differ in certain other ways. In respect to the depth of pigmentation of certain exposed areas of the skin (ears, soles of the feet, etc.), we have the same graded series as was observed in the case of pelage characters. *Polionotus*, *albifrons* and *leucocephalus* form a series of decreasing pigmentation. As regards the length of certain bodily appendages (tail and feet), *polionotus* gives

[1] Howell (1920), Sumner (1926).

the lowest values and *leucocephalus* the highest, with *albifrons* intermediate[1]. In ear length, the three races show no probable differences. Nor are there any certain differences in weight or in the mean length of the body (head + trunk).

Thus far, these sub-species have been spoken of as if they were homogeneous groups throughout the territory occupied by each. This may be approximately true in the case of *leucocephalus*[2], but it is quite untrue of either *polionotus* or *albifrons*. Even during the earlier field studies of 1924, three collections of *albifrons*, which were made at points more or less isolated from one another, showed undoubted and considerable mean differences in respect to pelage colour and other characters (Sumner, 1926, pp. 157–8). In 1927 a series of collections was made, extending from the dunes of the gulf coast, near St Andrews Bay, through the entire range of *albifrons*, to a point far within the range of *polionotus*. As already reported recently,[3] each of these races, particularly *albifrons*, displayed a very perceptible gradient from south to north, as regards the mean value of each of the pigmental characters which were subjected to quantitative treatment. A large and relatively abrupt change was, however, noted in the latter, at a point about 40 miles from the coast, where the transition from a somewhat atypical *albifrons* to a somewhat atypical *polionotus* occurred within the space of a few miles.

III. BREEDING EXPERIMENTS.

A limited stock of cage-bred animals was reared from each of the "pure" races. These "C_1" animals were utilised in some of the hybridisation experiments, and they also served a valuable purpose in showing the effects of captivity upon certain of the characters here considered. The great majority of the mice which were reared, however, were various sorts of hybrids between different sub-species. These are listed below. The numbers in parentheses represent the numbers which were reared to maturity, and the data from which have been included in the present discussion. In most of the groups, a small number of individuals have

[1] This intermediate position of *albifrons*, in respect to length of appendages, appears to hold only for the population dwelling in the immediate neighbourhood of the coast. Commencing at a point only 20 miles inland, the tail and feet of *albifrons* are no longer than those of *polionotus*. This fact is interesting in view of the fairly uniform gradient which seems to hold for all of the pigmental characters (Sumner, 1929, 1929 *a*).

[2] That is, so far as *local* variations are concerned. Of course there is a high degree of genetic variability within the population of any single locality.

[3] Sumner (1928 *a*, 1929, 1929 *a*).

been rejected, owing to being undersized, or to being manifestly stunted or deformed[1]. Some individuals which died in the cages were decomposed when found, and were thus not available for measurement. In the following list, the order in which the parent races are named has no significance. In each case, reciprocal crosses were obtained. Throughout this paper, the term "back-cross," when unqualified, refers to the first back-cross (commonly with *leucocephalus*), the term "grades" being applied to the second back-cross with *leucocephalus*.

Leucocephalus × *albifrons*[2],	F_1	(75)
,, ,,	F_2	(125)
,, ,,	back-cross, 3/4 *leucocephalus* ...	(70)
,, ,,	back-cross, 3/4 *albifrons*	(15)
,, ,,	grades, 7/8 *leucocephalus*	(58)
,, ,,	F_3	(65)
Leucocephalus × *polionotus*,	F_1	(74)
,, ,,	F_2	(109)
,, ,,	back-cross, 3/4 *leucocephalus* ...	(67)
,, ,,	back-cross, 3/4 *polionotus*	(16)
,, ,,	grades, 7/8 *leucocephalus*	(55)
,, ,,	F_3	(82)
Polionotus × *albifrons*,	F_1	(95)
,, ,,	back-cross, 3/4 *polionotus*	(76)
,, ,,	back-cross, 3/4 *albifrons*	(51)

In mating F_1 mice for the production of the F_2 generations, sibs were employed wherever possible, *i.e.* in the great majority of cases. No selection with reference to colour characters was practised. The F_3 generations, on the other hand, resulted from the matings of F_2 individuals which had been selected according to shade. About equal numbers of individuals of "dark," "medium" and "pale" parentage were reared.

In addition to the foregoing sub-specific crosses, I made a number of attempts to obtain inter-specific hybrids between *leucocephalus* and sub-species of *P. maniculatus*. The attempt succeeded in only a single case, as a result of which I obtained a fertile female hybrid between *P. maniculatus sonoriensis* and *P. polionotus leucocephalus*. This F_1 female was successfully back-crossed to a *leucocephalus* male, giving

[1] In dealing with this species, animals have been arbitrarily classed as "undersized" which fell below a body length of 74 mm. (males) or 76 mm. (females). In addition to the exclusion of all measurements from such mice, the measurements of body parts, though not of colour characters, have been rejected in the case of a small number of others which were obviously deformed. The total number of animals whose measurements have been excluded wholly or in part for these reasons is less than 4 per cent. of the cage-bred animals.

[2] In the following pages, I have dealt separately with the derivatives of the "East Pass" and "Foster's Bank" series of *albifrons*. A large majority of individuals, in each generation, belong to the former class (fifty-nine and sixteen, respectively, in the F_1), and it is these which have chiefly been reckoned with in dealing with this cross.

birth to two young, and to a *maniculatus* male (not, however, *sonoriensis*, but *gambelii*[1]), giving birth to thirteen young.

Reference has been made in preceding papers (Sumner, 1915, 1918*a*; Sumner and Huestis, 1921) to the not altogether normal character of the generations reared in captivity. There is a tendency toward reduction in total size, as well as toward a diminution in the relative length of the tail and feet. These conditions are believed to be in part of a rachitic nature. Since the fall of 1924 cod-liver oil has been regularly included in the dietary of the mice, being given in a mush which likewise contains milk. Although no carefully controlled experiments have been made to test the effect of this substance, it appears to have had a beneficial influence. Scarcely any of the more extreme cases of stunting and deformation, such as appeared in each of the series of animals before administration of cod-liver oil to the mothers, are to be found among those reared after the treatment was commenced[2].

Comparisons have been made between the mean values for the "wild" generation of each of the pure races and the corresponding values for the first cage-bred generation, after rejection of the small percentage of obviously stunted or malformed individuals (see above). What seems a fairer comparison has also been made between the mean values for the cage-bred mice and the means for those wild ones which actually figured as parents, the latter being weighted by the number of their offspring. While it does not seem worth while to present these figures in detail, it may be said that considerable differences appear between the two generations in certain cases. These differences, however, are not, on the whole, consistent. They may be of opposite sign in the different races, and even in the two sexes of the same race. For the most part, they are probably due to random sampling, the number of individuals, and especially of parents, being rather small. On the other hand, it seems likely that the preponderant tendency toward reduction in total size, and in the relative size of certain parts, is real. It accords with what has been observed on a more pronounced scale when the conditions of life have been distinctly unfavourable. Effects of captivity upon pigmental characters are much more problematic. If they exist at all, they are small in comparison with racial differences, and probably do not affect the interpretation of any of the results to be discussed below. This cannot be said unreservedly of such characters as tail and foot length.

[1] No fertile male *sonoriensis* was available at this time.

[2] However, the majority of those born "before using" are of normal appearance, and their *average* size is only slightly less than those born "after using."

IV. Detailed results from the various crosses.

(*a*) *The* leucocephalus-albifrons *series*.

(Text-figs. 1–10; Plates VIII, IX, X.)

Tables I and III give the mean values and standard deviations for the parent races and various hybrid generations concerned in this cross. As has already been stated, the *albifrons* material collected during the summer of 1924 came from three distinct localities more or less isolated from one another. While it was recognised in the field that these sub-races displayed certain mean differences in respect to colour and some other characters, the extent of these differences (see Text-fig. 1) was unfortunately not realised until after the first generation of hybrids had been reared. As a result individuals derived from two of these localities were employed indiscriminately as parents of the F_1 hybrids in the crosses with *leucocephalus*. In view of the surprisingly large differences between these two *albifrons* stocks, it has been found desirable, for most purposes, to separate the "East Pass" and "Foster's Bank" derivatives[1]. A large majority belong to the former series, while the residuum of Foster's Bank material is not large enough to have any great statistical value.

The results of reciprocal crosses, here and elsewhere, have been thrown together and treated, in each case, as a single population. This procedure seems justified, owing to the apparent lack of any significant differences depending upon the direction of the cross. Mean differences of some magnitude appear in certain cases, but these show no consistent trend, and are doubtless due to chance. The number resulting from one reciprocal cross is sometimes considerably smaller than that from the other, and may be inadequate to reveal any except pronounced differences. Such differences, as already stated, are probably not present among these hybrids.

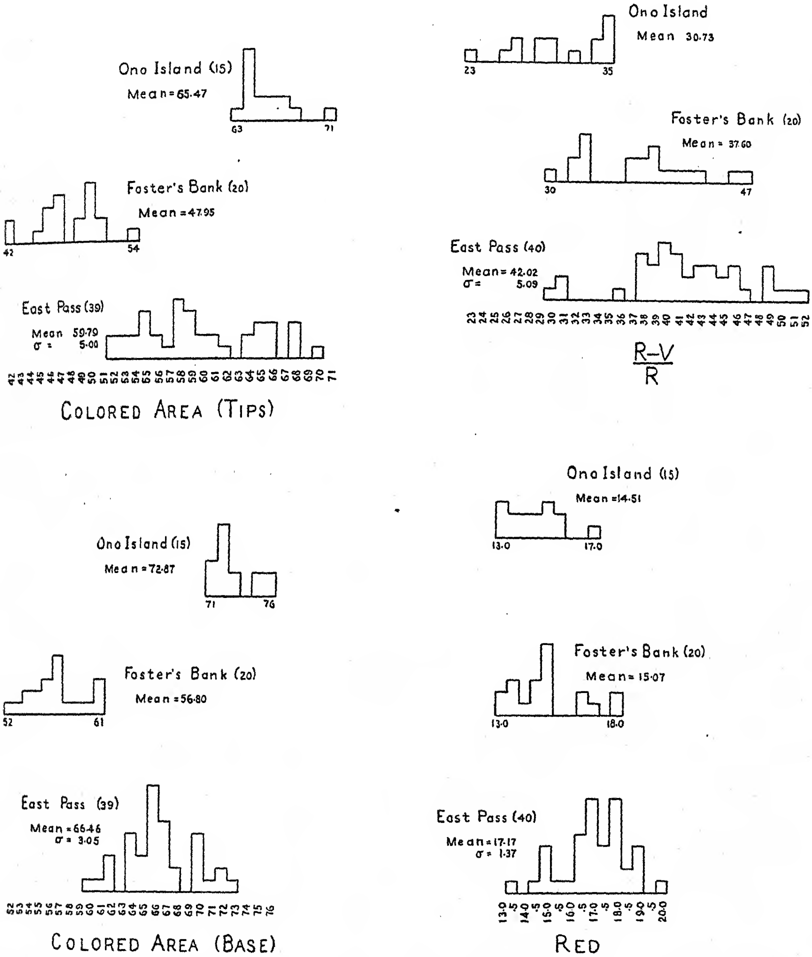
It will be most instructive, perhaps, to deal seriatim with the various measured "characters" which are represented in Table I.

Body length. As regards both this measurement and *weight* no significant racial differences are to be found between these two sub-species. There is no evidence of heterosis in the F_1 generation, nor any significant increase of variability in the F_2. I have more than once called attention to the greater mean size of the females of *Peromyscus* as compared with the males. This appears to be particularly true of the *polionotus* group.

[1] For the position of these localities see Sumner (1926).

Tail length. No facts of genetic interest are to be noted in the present cross in relation to this appendage.

Foot length. In this case there is a rather pronounced racial difference[1]. *Leucocephalus* has a greater mean foot length than any of the collections



Text-fig. 1. Pelage characters of three local collections of *Peromyscus polionotus albifrons*. Here and elsewhere, each square represents an individual.

of *albifrons*, the difference being most prominent when comparison is made with the East Pass series. There is, notwithstanding, no increase of variability in the F_2 generation over the F_1. Indeed we find just the

[1] It is possible to compare only individuals of the same sex, since males have relatively larger feet than females.

opposite relation in both sexes, though these differences have no statistical significance. In this connection it should be stated that genetic differences in foot length are masked by a high degree of non-genetic variability. The weighted mean of the coefficients of parent-offspring correlation between two generations of the "pure" races employed in this cross, together with those between the F_1 and F_2 hybrid generations, is only + 0·076. This is based upon 210 offspring. The corresponding figure for the coloured area, in the same series of animals, is 0·501[1].

Ear length. Nothing instructive is to be noted here.

Skeletal measurements. As regards these, a number of differences between these sub-species are shown, some of which are perhaps of statistical significance. These measurements seem to show that *albifrons* (at least from East Pass) has a slightly greater number of caudal vertebrae than *leucocephalus*, as well as a slightly longer pelvis and shorter skull. There is, however, no pronounced tendency for these characters to give intermediate values in the F_1 generation of hybrids, and there is certainly no tendency for the F_2 generation to show a higher range of variability than the F_1.

When we pass to characters relating to pigmentation of the hair or skin, a wholly different situation is found. In respect to all of these characters, so far as determined, there are racial differences of considerable magnitude, while a comparison of the various hybrid generations reveals many facts of genetic interest.

Tail stripe. This longitudinal stripe of dark hairs is present on the dorsal surface of the tail in most species of *Peromyscus*, as well as in some other genera of rodents. It is, however, totally lacking in *leucocephalus*, the tail of which is entirely white, and it is present in *albifrons* in a much reduced condition, or may be lacking altogether. It has been pointed out in earlier papers (1915, 1918, 1927, etc.; also Grinnell, 1922) that the relative width of this stripe undergoes interesting local variations within certain species. In general, dark races have a noticeably broader stripe than paler ones. In *P. p. albifrons*, and in certain hybrids where the tail stripe is usually incomplete, its length rather than its width has been determined, and this has been expressed as a percentage of the length of the entire (exposed) part of the tail. This percentage may vary from 0 to 100. Figures based on length alone do not, of course, adequately express differences in the degree of pigmentation of this stripe, since they represent only one dimension, whereas the stripe may be said

[1] In the case of foot length, certain of the generations are not available for parent offspring correlations owing to practical considerations which need not here be discussed.

to have three dimensions (that is, if the *depth* of pigmentation may be counted as one of these). Thus a "100 per cent." stripe in *albifrons* is, at best, much less of a stripe than is the 100 per cent. stripe found in most *P. p. polionotus*, which is both wider and of a deeper shade. Furthermore, the stated length of an incomplete tail stripe is often merely a rough approximation, owing to the rather arbitrarily chosen termination, which is unavoidable in cases where scattered black hairs occur throughout much of the length of the tail. After making due allowance for these difficulties, however, the length of the tail stripe is still to be regarded as a highly important character in the study of sub-specific hybrids in *P. polionotus*. Its range of individual variability far exceeds that due to observational error, and the genetic nature of many of the differences is obvious from an inspection of some of the graphs.

An extraordinary difference is to be noted in the tail stripe length of the two local collections of *albifrons* used in the present hybridisation experiments. Whereas the East Pass collection gives values from 7 to 100, with a mean of 41·73, the series from Foster's Bank for the most part lacks a tail stripe altogether, the highest value being 7. It is obviously necessary to treat these two groups separately.

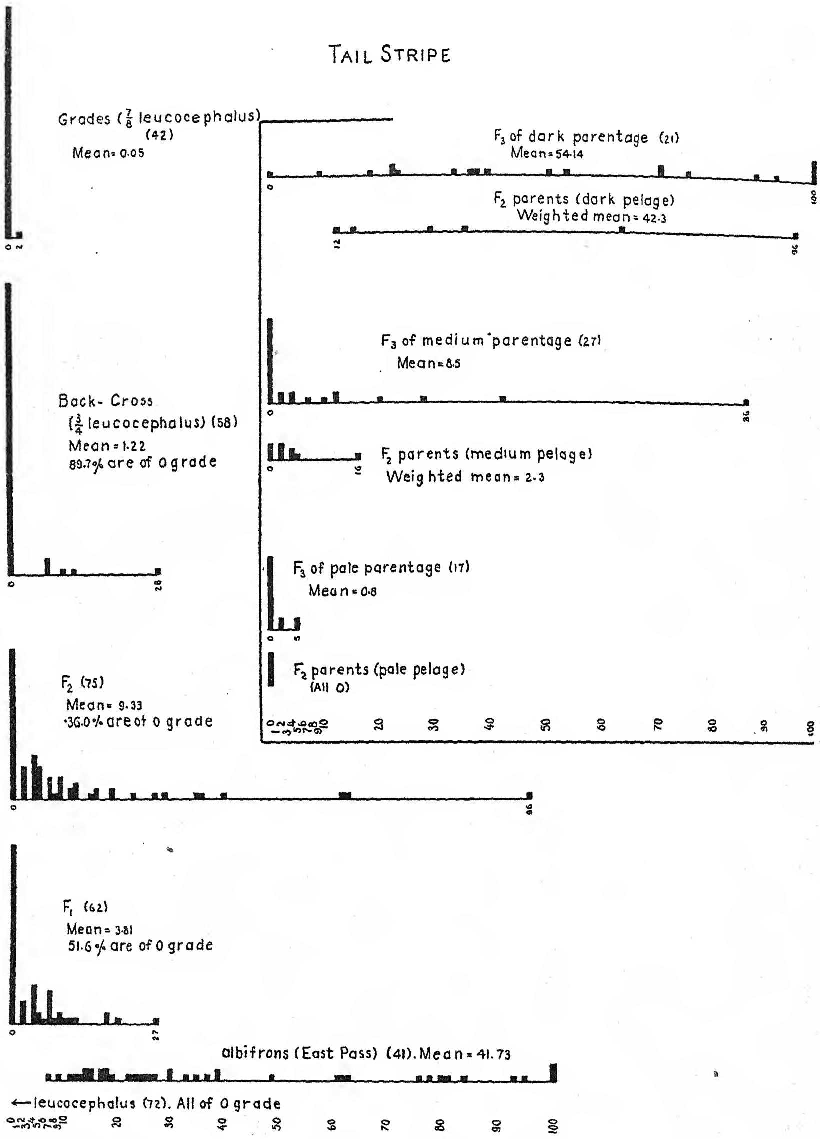
Text-fig. 2 shows the various generations which have been derived from crossing *leucocephalus* with East Pass *albifrons*. The mid-value between that of the two parental means (0 and 41·73) is about 21. We find, however, in the F_1 generation, a mean of 3·81, while slightly more than half of this generation are of the 0 grade[1]. Thus, lack of a tail stripe is incompletely dominant over its presence, a fact which will be illustrated in a number of ways later.

Comparison between the F_1 and F_2 generations is highly instructive. Whereas in the former the highest value is 27, in the latter we have seven cases exceeding that value, while the highest reaches 96. The mean, likewise, has advanced from 3·81 to 9·33, while only 36 per cent. of the individuals are now of the 0 grade[2]. All of these relations are, of course, in keeping with the above supposition that we have to do with an incomplete dominance of absence of tail stripe over its presence, and with the reappearance in the F_2 generation of individuals which are homozygous for some of the recessive factors.

Standard deviations have been computed for this character in the

[1] That this is not due to the accidental choice of *albifrons* parents having low-grade tail stripes is shown by the mean figure of the latter (weighted by the number of their offspring). This figure is 40·42.

[2] The weighted mean of the values for the F_1 parents is 4·29.



Text-fig. 2. Tail stripe values for *leucocephalus* (0), *albifrons* of the East Pass series, and the various generations of hybrids. Here and elsewhere, the values given for length of tail stripe represent percentages of the total exposed part of the tail.

various generations, though this is scarcely a legitimate procedure, owing to the extreme asymmetry of the distributions. It is obvious, however, that the variability is far greater in the F_2 generation than in the F_1.

Back-crosses with the paler parent race (*leucocephalus*) give a mean value for the tail stripe of 1·22, while 90 per cent. of the individuals are of the 0 grade. For the "grades" (7/8 *leucocephalus*), all but one of the forty-two individuals belong to the 0 grade, the single exception giving the lowest measurable grade (2).

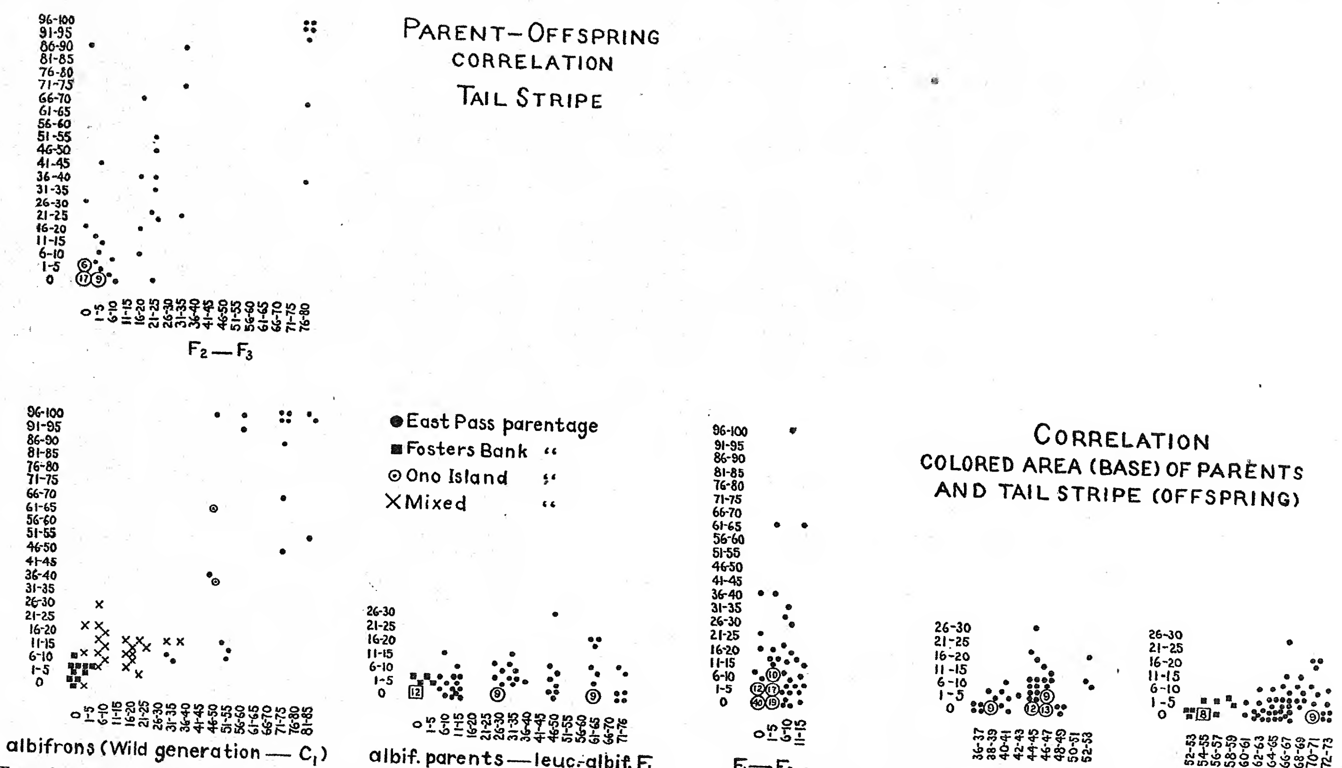
It is a matter of interest that the degree of dominance is nearly alike in the two generations in which it is possible to test this. Thus the mean value for the F_1 generation (3·8) is removed only nine hundredths of the distance from 0 to the weighted mean of the *albifrons* parents (40·42), while the mean of the back-cross generation (1·22) is eleven hundredths of the distance from 0 to the weighted mean of the F_1 parents of that generation (10·71)[1]. It happens that all of the back-cross parents of the "grades" lacked the stripe in any measurable degree, and this condition is virtually repeated in the latter generation.

The limited series of crosses derived from *albifrons* of the Fo[illegible]'s Bank series are far less instructive. Only four individuals out o[illegible] collection were employed as parents, three of these having a tail str[illegible] of the 0 grade. The F_1 hybrids between these and *leucocephalus* numbered only sixteen, while the F_2 generation numbered twenty-nine, the back-crosses with *leucocephalus* twelve, and the grades seventeen[2]. Certain of the relations shown by this series are contradictory, owing probably to the limited numbers (*e.g.* the lower variability of the F_2 generation as compared with the F_1). It is significant, however, that the great majority of individuals, both in the F_1 and F_2 generations, are of the 0 grade, while the highest value in either generation is 5. The slight development of the tail stripe in the Foster's Bank mice thus represents a hereditary difference.

The point last referred to brings up the question how far, in general, these differences in the development of the tail stripe are hereditary. Within the East Pass series alone, the values range from 7 to 100, while individuals giving values from 9 to 76 were mated with *leucocephalus* as parents of the F_1 hybrids. It may seem that little of an instructive nature can be learned from the use of such heterogeneous material.

[1] Several F_1 mice having relatively high tail-stripe values figured as the parents of a considerable proportion of the back-cross generation.

[2] In addition to these last, there are twenty-one F_2 individuals of mixed descent, these having both East Pass and Foster's Bank grandparents.



Text-fig. 3. Correlations between tail stripe (parents) and tail stripe (offspring), and between coloured area (parents) and tail stripe (offspring) in the *leucocephalus-albifrons* cross. Abscissas denote mean value of parents; ordinates the individual offspring. Derivation of *albifrons* stock is indicated by symbols in first, second, and fourth figures of lower row; in the other two figures no distinction is made. Where the number at a given locus is too great to be represented by individual dots, this is indicated by the figure in the circle or square.

However, there is abundant evidence that these great differences within a single local population are largely non-genetic.

Owing to the great variability of this character, and to its asymmetrical distribution, the computation of parent-offspring correlations would not here be justified. But the correlation may none the less be portrayed graphically (Text-figs. 2, 3). In Text-fig. 2 we have the values exhibited by an F_3 generation of selected parentage. As already stated (p. 282), the "pale," "medium" and "dark" sections of the F_3 generation were derived from F_2 parents which had been selected according to the shade and extent of the coloured area of the pelage. The magnitude of the tail stripe played little or no part in the choice. The conditions here portrayed make it clear both that the differences in the length of the tail stripe are in part genetic, and that they are closely correlated with differences in the general pigmentation of the pelage.

Text-fig. 3 further illustrates the undoubted, though feeble and erratic, correlation which exists between parents and offspring in respect of the degree of development of the tail stripe.

Allowing, then, for great differences in the "expression" of this character, due to non-genetic causes, is it possible to estimate the number of genetic factors concerned in the difference between total lack of a tail stripe and its presence *in any degree*? Comparison between the arrays for the F_1 and F_2 generations (Text-fig. 2) makes it quite unlikely that we have to do with a simple one-factor difference. In the F_2 generation we should have 25 per cent. of pure dominants, all of which would be of 0 grade, according to hypothesis. But to this number should be added half of the heterozygotes, since about that proportion of F_1 animals were of 0 grade in this respect. Thus, about 50 per cent. of 0 grade individuals, instead of the 36 per cent. actually found, would be expected in the F_2 generation, if we had to do with a one-factor difference.

That the entire difference between the *leucocephalus* and the *albifrons* condition, in respect to tail stripe, is not due to a single pair of allelomorphs is even more certain. When each of the forty-eight F_2 individuals which display this character is compared with its own *albifrons* grandparent, we find that in only three cases is the value equal to or greater than that of this grandparent. No others approach the latter very closely. Although this does not, of course, constitute an accurate estimate of the number of pure segregants for the character in question, the number is obviously far too small for a monohybrid ratio. On the hypothesis of a single factor difference, about nineteen individuals, out

of the seventy-five in the F_2 generation, should be homozygous for the *albifrons* tail stripe factor. The number actually found lies between the expected numbers for two and for three factors. We shall find reasons for believing that even that estimate would be too low.

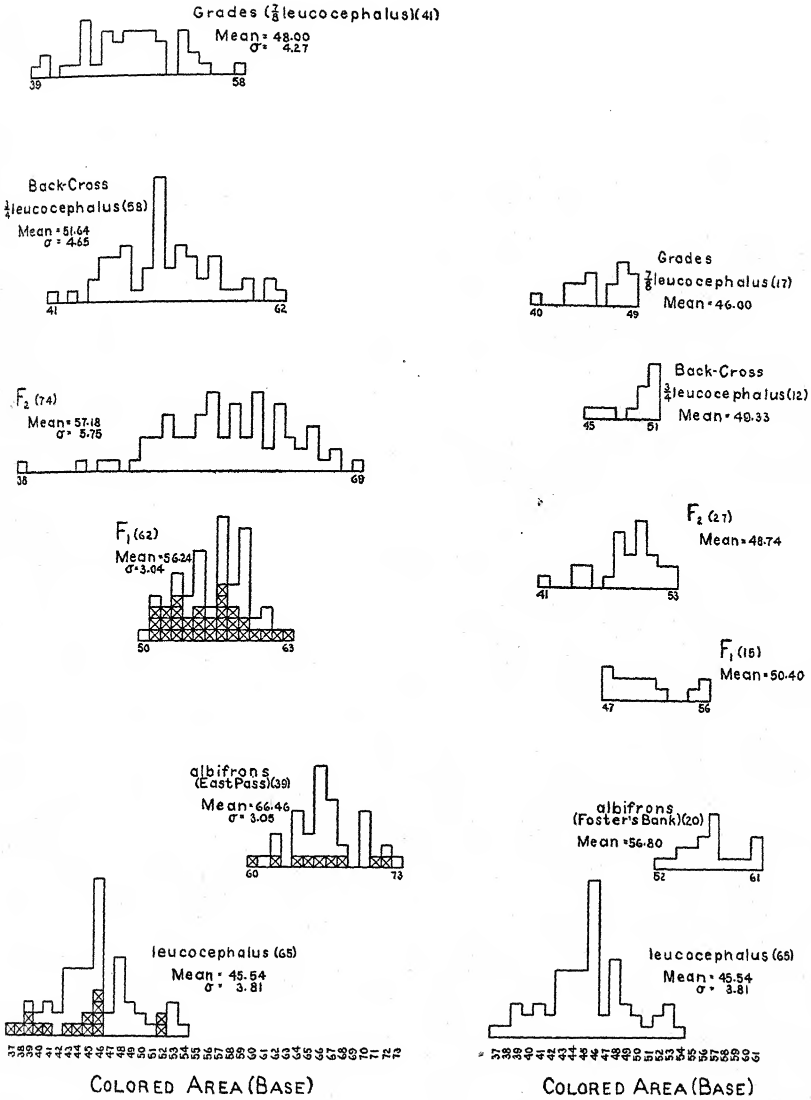
Foot pigmentation. Owing to the complete lack of pigmentation in the foot of *leucocephalus*, and its merely occasional presence in *albifrons*, this character cannot profitably be considered in the present cross. Reference will be made here only to the higher mean value found in all of these generations of *leucocephalus-albifrons* hybrids, in comparison even with *albifrons* itself. This fact will be referred to in connection with the next cross.

Coloured area of the pelage. As stated above, the entire ventral and portions of the lateral surfaces of the body, in both *leucocephalus* and *albifrons*, are clad with hairs which are white from base to tip. In contrast to this area (peripheral in the flat skin), is a dorsal (central) region, in which the hair is pigmented, partly at the base only, but for the most part throughout its entire length. Thus, when examined by transmitted light, and viewed from the inside of the skin, a central, semi-opaque area is seen, which is bordered by a translucent margin of varying width. The former is constituted by all the pigmented hairs of the pelage, including both those which are pigmented at the base only, and those which are pigmented from base to tip. The semi-opaque area thus seen is usually outlined rather sharply, and may be measured by means of a planimeter. When stated as a percentage of the entire area of the animal's skin it is a character of prime importance[1].

The mean value of this character in *leucocephalus* is 45·54, extreme variants ranging from 37 to 54. In *albifrons* of the East Pass series, the mean is 66·46, the range in variation being from 60 to 73. The *albifrons* from Foster's Bank show a far lower value, the mean being 56·80, and the range from 52 to 61. Finally, the small Ono Island series (not used in the hybridisation experiment) give the high mean value of 72·87. Fortunately, most of the hybrids were derived from crosses with the East Pass series, in which the range of variability is relatively small and does not closely approach that of *leucocephalus*.

Text-fig. 4 shows the behaviour of this character in the various generations of hybrids (excluding the F_3), while the means and standard deviations appear in Tables I and III. The mean value for the sixty-two

[1] Sumner (1926, 1927). Values thus obtained are obviously far from being absolute ones. Since the procedure is constant, they are, however, strictly comparable with one another..



Text-fig. 4. Values for coloured area of pelage (here the area occupied by hairs pigmented at base) for *leucocephalus*, *albifrons* (of two local sub-races) and the various hybrid generations, excluding F_3. Cross-hatched squares represent parents of the next generation.

F_1 mice (56·24) is very nearly an average of the weighted means of the *leucocephalus* and *albifrons* parents. Thus, there is no appreciable tendency toward dominance in respect to this character. In accordance with the latter fact there has been no appreciable shifting of the mean in the F_2 generation. The slight difference found is probably of no significance.

There is, however, an obvious and very considerable increase in variability when we pass to the second hybrid generation. The latter (seventy-four skins available) has a range from 38 to 69, with a standard deviation of 5·75, whereas these values, in the F_1 generation, range from 50 to 63, giving a standard deviation of 3·04. The two lowest values in the F_2 fall below the mean value for *leucocephalus*, while the three highest values equal or exceed the mean for *albifrons*[1].

In the back-cross (F_1 × *leucocephalus*, in either direction), the fifty-eight animals show a range from 41 to 62, a mean of 51·64, and a standard deviation of 4·65. The mean is approximately midway between the mean of *leucocephalus* (wild generation) and that of the F_1 generation, while the variability is higher than in the F_1, though lower than in the F_2. Four individuals give values equal to or below the mean for *leucocephalus*, while none reach the mean for *albifrons*.

The small group (fifteen) of back-crosses with the other parent race (*i.e.* 3/4 *albifrons*) give a range of from 52 to 69, and a mean of 61·27. This figure is very nearly midway between the F_1 mean and that of the East Pass *albifrons*. The *albifrons* parents and grandparents of this group were almost wholly East Pass derivatives.

Of the second back-crosses or "grades" (first back-cross × *leucocephalus*, in either direction), we have forty-one individuals, giving a mean of 48 and a standard deviation of 4·27. The mean is approximately midway between the mean of the back-cross generation and that of *leucocephalus*.

Passing to the limited number of hybrids involving the Foster's Bank series of *albifrons*, it is evident (Text-fig. 4) that the mean value of the coloured area for this series is much closer to that for *leucocephalus* than is that for the East Pass series. Accordingly, the F_1 generation of hybrids likewise gives a much lower mean. The relations between the F_1 and the first and second back-crosses are such as might be expected,

[1] Unless otherwise specified, the mean of the entire population of a given parent generation is intended. While the weighted mean of the actual parents is probably a fairer index of the latter's genetic contribution, this has not always been computed, owing to the labour involved, as well as to the fact that such means commonly differ but little from those of the total population to which the parents belong.

considering the small numbers of individuals. The difference between the F_1 and F_2 means is unexpected, but this probably has no significance.

The facts discussed in the last few paragraphs make it plain that the differences between *leucocephalus* and either strain of *albifrons*, in respect to the extent of the coloured area of the pelage, are not dependent upon a single pair of Mendelian factors. If we may assume that they are explainable on a Mendelian basis at all, one naturally enquires whether the number of factor differences may be determined.

It has already been stated that two F_2 individuals of the *leucocephalus*-East Pass cross fall below the mean value of *leucocephalus*. Indeed one gives a value as low as any but the palest single specimen of *leucocephalus*. However, in view of the wide range of variation within *leucocephalus* itself, it is more pertinent to ask how many F_2 animals give values equal to or lower than *their own leucocephalus grandparents*. It happens that there are two such, these being the same two individuals as have already been referred to. One gives a value equal to that of its *leucocephalus* grandparent, the other a value one unit less.

It would, of course, be unjustifiable to conclude forthwith that these particular two individuals, and no others, are pure segregants for the factors concerned in determining the racial differences in the magnitude of the coloured area. For, in the first place, even an individual having the same genetic constitution as a given ancestor would not necessarily agree with the latter precisely. It might give a lower or higher value, and a departure in either direction would be equally probable. We should not be warranted, therefore, in including only those individuals which equalled or *surpassed* their parents in respect to a given character, since this number would tend to be too low[1].

However, there is another circumstance working in the opposite direction. If we suppose that a number of factor differences are concerned here, it is likely that the various genetic classes in the segregating generations would overlap rather broadly, owing to non-genetic variability. For this reason, an individual not homozygous for all of the colour-restricting factors derived from *leucocephalus* might nevertheless equal or surpass its *leucocephalus* ancestor in respect to the character in question.

Since we have no means of determining which of these two opposing tendencies would exert the greater influence, let us make the arbitrary

[1] The word *surpass* is here employed in the sense of having a *smaller* value for coloured area than the *leucocephalus* ancestor, since *leucocephalus* differs in this direction from *albifrons*.

assumption that their effects would balance one another, and provisionally count as pure *leucocephalus* segregants (for these factors only) the actual number of individuals which give equal or lower values than their *leucocephalus* ancestors.

Thus, as already stated, we have, in the present F_2 generation, two segregants supposedly "pure" for the *leucocephalus* allelomorphs which influence the magnitude of the coloured area. This frequency (1 in 37), stands between the expected frequencies in cases where two and three pairs of Mendelian factors are concerned in a cross. However, in the other direction, it happens that not one of the F_2 individuals attains as *high* a grade as its *albifrons* grandparent. This would lead us to suspect that we have to do with more than two factor differences.

Passing to the back-crosses with *leucocephalus*, we find but a single individual, out of a total of fifty-eight, which gives a lower value than the mean of its *leucocephalus* ancestors. This is not far from the proportion of 1 in 64, which would be the expected proportion were six factor differences concerned in the cross.

The "grades" (7/8 *leucocephalus*) yield seven cases, out of a total of forty-one, in which the extent of the coloured area equals or falls below that of their *leucocephalus* ancestors. Thus we have about 17 per cent., a proportion very close to that to be expected were six factors concerned (see Text-fig. 15). This is in close agreement with the figure indicated by the back-cross generation, but not at all in harmony with that which might be inferred from the number of *leucocephalus* segregants in the F_2 generation. Needless to say, none of these figures have any great measure of probability, owing to the small numbers concerned, and to the further uncertain elements in the situation which have been referred to above.

One weighty reason for believing that we have to do here with a considerable number of factor differences is based upon the distribution of cases in the population of "grades" (7/8 *leucocephalus*). For purposes of comparison I have computed the expected proportions belonging to each phenotypic class, which would result from such a cross, on the supposition that we had to do with two to ten pairs of factors respectively[1]. The proportional numbers of these classes, expressed in per-

[1] The terms of this series are derived from the expansion of $(1+3)^n$, where n equals the number of supposed allelomorphic pairs concerned. If the more heavily pigmented race (in this case *albifrons*) be represented as $AABBCC...$, etc., and the less heavily pigmented race (*leucocephalus*) be represented as $aabbcc...$, etc., the frequencies plotted in these graphs are those for genetic combinations containing the various possible numbers of capital letters, ranging from the completely heterozygous condition ($AaBbCc...$, etc.) to a

centages, are shown graphically in Text-fig. 15. It is evident from this figure that a very asymmetrical distribution is to be expected until about five or six factors are reached. Furthermore, the asymmetry is of such a nature that the mode is displaced in the direction of the pure race to which the hybrids have been successively crossed. Thus, in the present case, if only a few factor differences were concerned, the genetic classes which approach most closely to "pure" *leucocephalus* should be piled up on one side of the distribution surface, while those classes which show the effects of the cross with *albifrons* should be present in gradually decreasing numbers, tapering off to a low minimum for the completely heterozygous class, equivalent to the F_1.

This asymmetry is so marked in all of the polygons up to those for five or six factors that it should manifest itself even in the small population (forty-one individuals) with which we have to deal in the present case, and even when we take account of the considerable amount of non-genetic variability and of probable departures from the ideal scheme assumed in the preceding footnote. A glance at Text-fig. 4 shows that nothing of the sort has occurred. The distribution is approximately symmetrical. This same fact will be referred to again in connection with another character in the present cross, and with both characters in another cross.

Considerable asymmetry is to be noted in the small series of Foster's Bank crosses, but this asymmetry is not of the type which is called for by the considerations here discussed, and it is likewise manifested in generations where it should not occur. The relations are probably accidental.

In the foregoing argument, both *leucocephalus* and *albifrons* were treated provisionally as if they were genetically homogeneous in respect to the character under consideration. As might have been anticipated, this is distinctly not the case, a fact which serves to further complicate the picture presented to us.

Parent-offspring correlations for the "pure" races and the various generations of hybrids have been computed for this and some other

condition homozygous for the *leucocephalus* factors (*aabbcc*..., etc.). Any strict comparison between these polygons and the frequency distributions in an actual 7/8 cross involves, of course, several assumptions, viz. that Aa is approximately midway between AA and aa; that the effects of A, B, C, etc. are approximately equal; and finally that all of the "capital" genes belong to one of the two sub-species, while all of the "lower case" ones belong to the other. Since, however, we are not trying to determine the actual number of factors concerned, even roughly, but merely endeavouring to set a minimum value for these, I believe that the foregoing objections may fairly be waived.

characters. The weighted mean of these coefficients of correlation between the successive generations (excluding that between F_2 and F_3) is + 0·375. The degree of correlation is doubtless somewhat increased by the fact that the derivatives of the local sub-races of *albifrons* have not been segregated from one another in these computations[1].

The correlation between selected groups of F_2 individuals and their F_3 offspring (see p. 282) is + 0·751. The high value of this coefficient is due to the fact that three groups, representing the extremes of shade and the medium condition, were selected, and were subjected to assortative mating. The effect upon the correlation was, of course, much the same as if several pairs of pure *leucocephalus* and *albifrons* had been included among the F_2 parents.

Graphs (Text-fig. 6) showing the distribution of these offspring of selected F_2 parents are instructive[2]. The wide differences between these group means is obvious.

Red. This is the value of the reading obtained through the red colour screen in the Ives Tint Photometer. It is expressed as a percentage of the light which is simultaneously reflected from a standard white block (magnesium carbonate). The value obtained with the red screen is employed in preference to those obtained with either of the others used by me merely because it is the highest of these values. In the present discussion it is employed merely as an index of the paleness or darkness of the pelage, high values denoting pale skins and *vice-versa*[3].

From Table I and Text-fig. 5 it appears that *leucocephalus* gives a mean value for this character of 25·4, the individual figures ranging from 20 to 37. The East Pass collection of *albifrons* gives a mean of 17·17, the range being from 13·5 to 20. There is no overlapping between the actual parents of the F_1 generation, the lowest value for *leucocephalus* being 21·5, the highest for *albifrons* being 19.

The mean value of the Foster's Bank *albifrons* is 15·07, that of the fifteen Ono Island skins being 14·51.

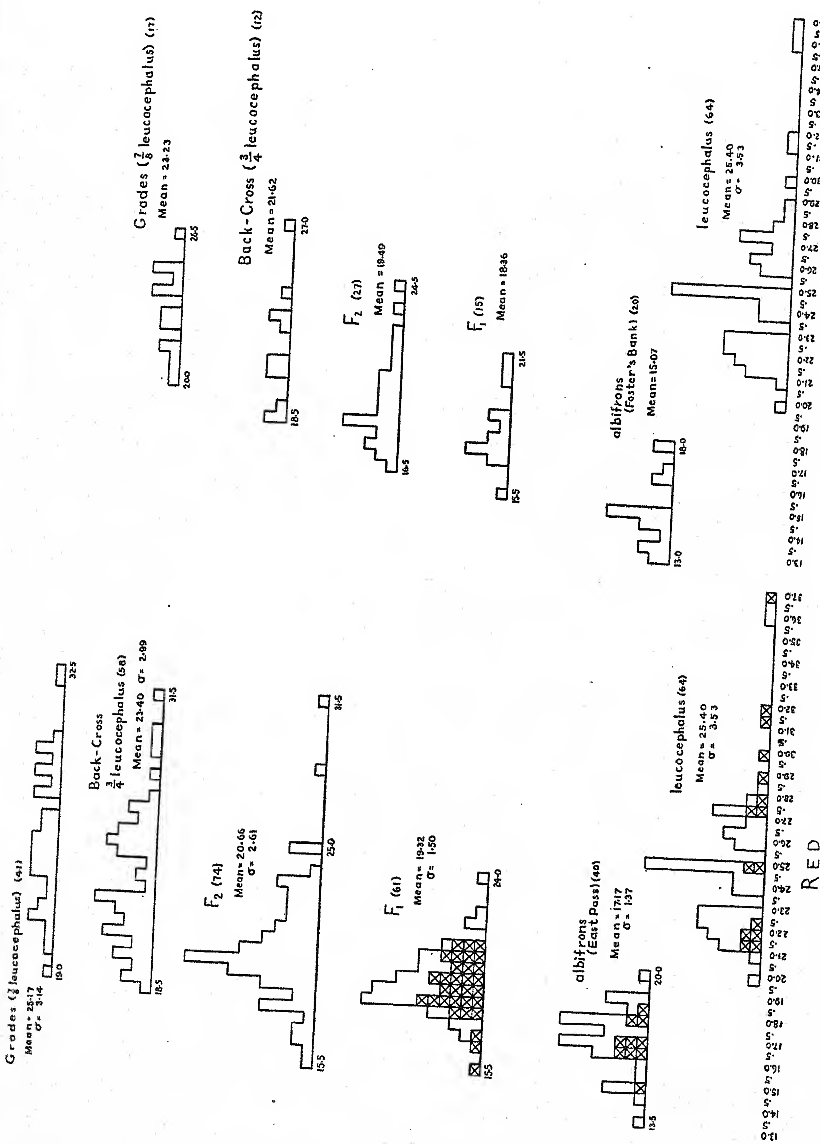
In the F_1 generation of the *leucocephalus*-East Pass cross we have a mean value of 19·32, the extremes being 15·5 and 24. The mean here

[1] The computations were well under way before the extent of these local differences was realised, and it has not been thought worth while to repeat these laborious calculations.

[2] Selections based upon the inspection of living animals, before their pelage measurements are known, are necessarily inexact.

[3] For an extended account of my procedure in using this instrument, see Sumner (1927). Let me repeat here that the colour values obtained in these studies are not absolute ones, nor do they approach the accuracy required in physics. All that is claimed is that the figures are reasonably comparable for the various series of skins here considered.

is appreciably lower than either the mid-value between the means of the parent races (21·28) or between the weighted means of the actual



Text-fig. 5. Values for "red" (readings through red colour-filter in the Ives Tint-Photometer) for the same populations represented in Text-fig. 4.

parents (21·41). It would thus appear that there is a slight tendency toward dominance of the darker condition over the paler, a relation

which will be found to be even more pronounced in the *leucocephalus-polionotus* cross to be described below. It is of interest to recall that this is just the reverse of the relation manifested in the case of tail stripe length, in which the unpigmented condition is incompletely dominant over the pigmented. This situation is the more curious, since depth of coat colour (which is merely the reciprocal of the value of "red") is positively and strongly correlated with tail stripe.

In the F_2 generation we meet with the following salient facts. The mean is 20·66, being thus somewhat higher than the mean for the F_1 generation as a whole (19·32), and still more so in comparison with the weighted mean of the parents of the F_2 animals (19·14). This difference, which appears to be significant, is in the expected direction, representing a shift in the direction of the recessive condition. The same relation has already been noted in the case of tail stripe, and will be met with again in the *leucocephalus-polionotus* cross.

More important still is the increase in variability. The standard deviation for "red" has risen from 1·50 in the F_1 to 2·61 in the F_2. Likewise, the upper limit of the range has risen from 24 to 31·5, there being two individuals far exceeding the mean condition in *leucocephalus*. The lowest values, however, are the same in the two generations.

In the back-cross between the F_1 generation and *leucocephalus*, we have a mean value for fifty-eight individuals of 23·4, and a standard deviation of 2·99. The highest single value is, however, no higher than in the F_2 generation. The small series (fifteen) comprised in the back-cross with *albifrons* is not comparable with the others, since two of the collections of *albifrons* are represented in their ancestry.

The "grades" (7/8 *leucocephalus*) give a mean value of 25·17, which is close to that for "pure" *leucocephalus*, while nearly half of the total number equal or exceed, in this character, the mean value for the latter race.

The conditions shown in the limited number of crosses between *leucocephalus* and the Foster's Bank series of *albifrons* are evident from inspection of the graphs. The same tendencies are manifest as in the East Pass derivatives, the differences being due (1) to the much smaller numbers in the former series, and (2) to the considerably lower mean value for "red."

Considering, as previously, the proportion of seemingly "pure" segregants in the various hybrid generations, we find that in the F_2 generation, three individuals of East Pass lineage give a value equal to and three a value higher than the *leucocephalus* grandparent. If these six were

regarded as segregants which were pure for the *leucocephalus* factors (see p. 296) we should have about one out of twelve in the total population, *i.e.* more than the expected number, if only two-factor differences were concerned.

Conversely, four F_2 individuals equal or *fall below* the value for the *albifrons* grandparent, *i.e.* about one in eighteen.

Among the back-crosses, we have twelve out of fifty-eight which would be "pure" segregants according to the suggested criterion, a proportion which would likewise correspond roughly with a two-factor difference[1].

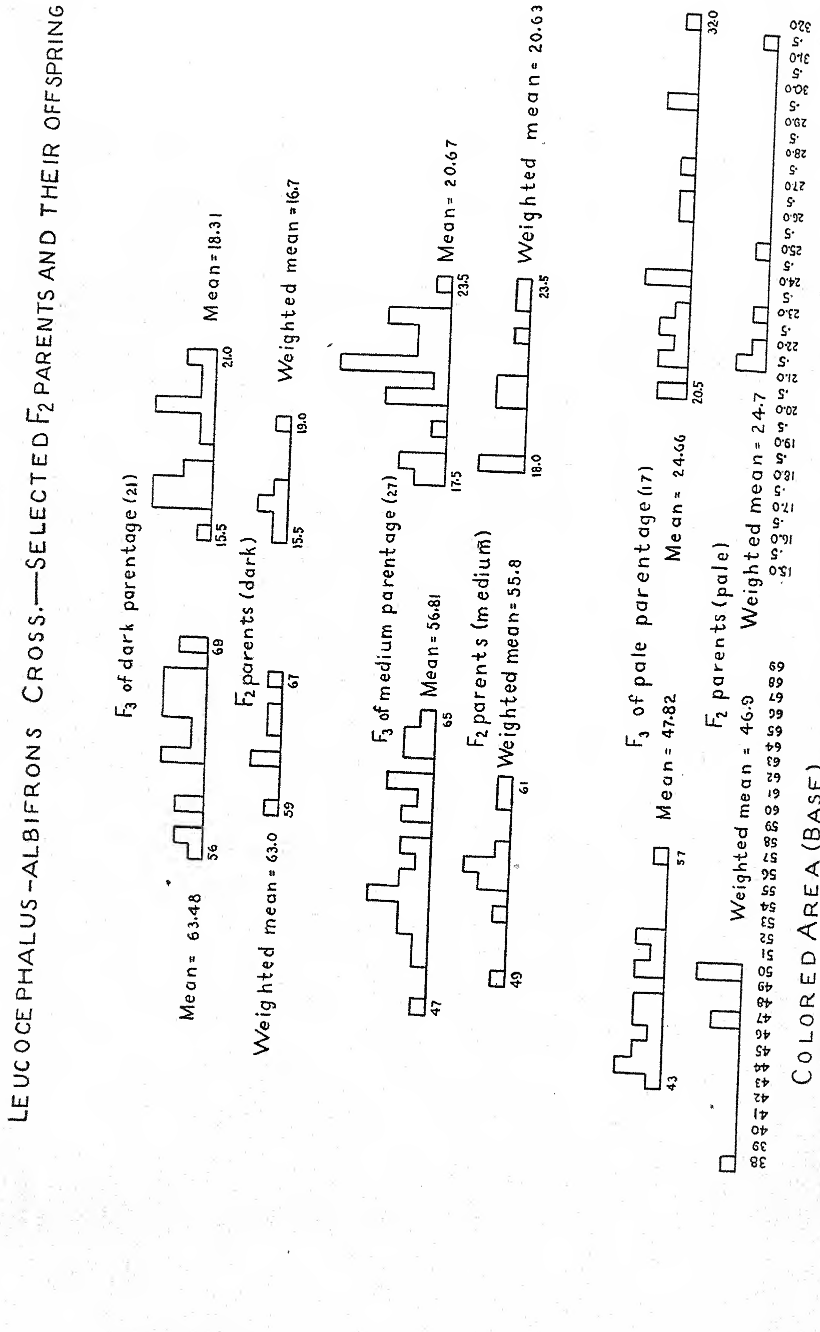
Passing to the "grades," we have nineteen individuals out of forty-one (about 46 per cent.) which reach or surpass the mean of the *leucocephalus* ancestors. The expected proportion of pure segregants resulting from such matings is 42·2 per cent., on the assumption that we have to do with three factor differences.

Thus, if the foregoing reasoning were to be accepted, we should have a character difference between these two sub-species which depends upon two or at most three principal pairs of Mendelian factors. This is quite unexpected in view of the fact that racial differences in the extent of the coloured area were found to depend almost certainly upon a considerably greater number of factors than this, and of the further fact, to be discussed later, that these two "characters" are probably dependent, to a large extent, upon the same factors.

Inspection of the distribution polygon for the generation of "grades" (Text-fig. 5) reveals no more evidence of a pronounced asymmetry of distribution than was to be observed in the distribution of values for "coloured area" (p. 297). As judged by this criterion, a moderately large number of factor differences must be concerned in the case. An effort to reconcile these various contradictions will be made after the other crosses have been considered.

Parent-offspring correlations comparable with those computed for coloured area (see above) give a weighted mean for the various generations (excluding the correlation between F_2 and F_3) of $+ 0·264$. This is a considerably lower figure than that for coloured area (0·375), a fact which probably depends upon the higher proportion of non-genetic variability in the character "red," as derived from tint-photometer readings of the pelages.

[1] Of these twelve, it is to be remarked that nine have as their mother (and likewise n some cases as grandmother) the same *leucocephalus* individual, and that the value of "red" for this individual is considerably below the average.



Text-fig. 6. Two pelage characters in selected F_2 parents and their F_3 offspring (*leucocephalus-albifrons* cross). The basis of selection was relative paleness or darkness, depending upon both depth and extensity of pigmentation.

The correlation between the selected series of F_3 animals and their F_2 parents is + 0·743. This is slightly, though not significantly, lower than that for coloured area. Text-fig. 6 gives the distribution of values in the offspring of each group of selected parents.

$\frac{A_b}{R}$. Since "red" is here used as an index of the paleness of the pelage, the reciprocal of this $\left(\frac{1}{R}\right)$ may be regarded as indicative of the depth of pigmentation. The total amount of pigment in the pelage is of course roughly proportional to the coloured area multiplied by the density of pigmentation, *i.e.* $A \times \frac{1}{R}$ or $\frac{A}{R}$.[1] This is, of course, far from being an exact quantitative expression for the amount of pigment present, and in any case it is obvious that we are not dealing here with another character, independent of both "coloured area" and "red," even supposing that the last two are independent of one another.

Of the two parent races here considered, *leucocephalus* gives a mean value of 1·82, *albifrons* (East Pass series) a mean value of 3·9. The figures for the weighted means of the actual parents are 1·72 and 3·95 respectively. The mean for the F_1 generation is 2·93, that for the F_2 being 2·82, which is slightly nearer the value for the paler of the two races (*leucocephalus*). The expected increase of variability in the second hybrid generation is to be observed here. Conditions with respect to the back-cross generation and the grades are made evident in Text-fig. 7 and Tables I and III.

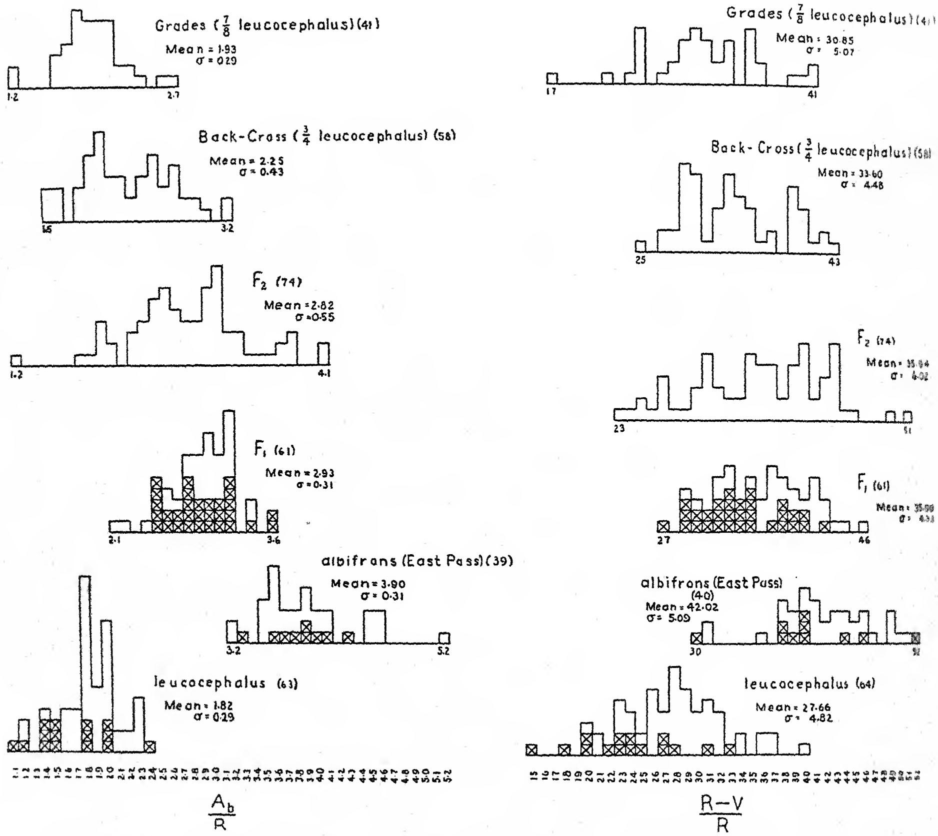
A quest for cases in which hybrid descendants have equalled or surpassed (here fallen *below*) their *leucocephalus* ancestors in respect to the value of $\frac{A}{R}$ results in contradictory findings. Whereas the number of supposedly pure segregants in the F_2 generation points to the presence of not more than three factor differences, the proportion among the grades is about that for six factors. The distribution of frequencies in the latter generation (Text-fig. 7) likewise points to a relatively large number of factors.

The weighted mean of the parent-offspring correlations for the two pure races here involved, and for the various hybrid generations (excluding that between F_2 and F_3), is + 0·312. This is intermediate between the figures for coloured area and red. The correlation between the selected F_2 parents and the F_3 generation is + 0·762. It was thought possible that this fraction $\frac{A}{R}$ would prove to be a better

[1] Sumner, 1929 $\left(\frac{Ca}{R}\right.$ was used in the former paper$\left.\right)$. I shall here designate the area of hair pigmented at the base by A_b, the area pigmented at tips being designated as A_t.

index of genetic differences in pelage pigmentation than either of the values from which it is derived. It is evident that this is not the case.

$\frac{R-V}{R}$. The exact meaning of this fraction has been explained in my recent paper on technique (1927), and need not be discussed at any length here[1]. Briefly speaking, the fraction represents an index of



Text-fig. 7. Values for fraction: coloured area ÷ red, and for index of saturation, in *leucocephalus*, *albifrons* (East Pass series), and hybrids (excluding F_3).

[1] Since there is no "free" blue or violet in the pelage of a mouse, the reading with the blue-violet screen (V) represents the amount of non-selective reflection, *i.e.* the amount of "white" light which is reflected from the skin. $R-V$ represents the amount of "free" red, after deducting that which is present as a component of the white light. In the paper referred to, this fraction was written "$\frac{R-BV}{R}$," but the formula here employed accords better with algebraic notation, since BV ("blue-violet") is a single quantity. In my first paper on the *polionotus* group (1926), I employed a different index $\left(\frac{R-V}{V}\right)$.

saturation as regards red. High values indicate a richly coloured skin (brown or yellowish), low values an approach to neutral grey. It will be found that these differences relate to a "character" which is to a considerable degree independent of the other pigmental "characters." Pale pelages may vary greatly in their richness of colour, and the same is true of dark ones. Certain correlations exist, however, between saturation and shade, as will be pointed out.

Leucocephalus, owing in part to the presence of large numbers of white hairs within the coloured area of the pelage, gives a low average value for this fraction (27·66); *albifrons* giving much higher values (East Pass, 42·02; Foster's Bank, 37·6; Ono Island, 30·73). Only the East Pass derivatives will be considered here.

In the F_1 generation we have a mean of 35·90, which does not differ widely from the mid-point between the means of the parent races (34·84). When, however, we compare the F_1 mean with the weighted mean of the actual parents of the F_1 generation, we have a considerably greater difference ($35{\cdot}90 - 31{\cdot}44 = 4{\cdot}46$). This would seem to imply a partial dominance of the more richly coloured condition over the greyer one, a relation which will be found to hold with yet greater force for the *leucocephalus-polionotus* cross.

The F_2 mean (35·94) is almost exactly the same as that for the F_1,[1] but there is a marked increase in variability, the standard deviation being 6·02, as compared with 4·33. The mean value for the back-cross generation is 33·60, this likewise being a figure far in excess of the mid-value between the weighted means of the *leucocephalus* and the F_1 parents of this generation (29·38). The mean for the grades (30·85), however, is very close to the weighted mean of their parents (31·08).

Decidedly curious relations are encountered when we consider the number of F_2 individuals which equal or surpass their grandparents in respect to this "character." On the one hand, there are five individuals out of seventy-four which give values equal to or lower than their *leucocephalus* grandparents; on the other hand, thirty-nine individuals, or more than 50 per cent., give values equal to or higher than their *albifrons* grandparents! Furthermore, even in the F_1 generation, there are two individuals which fall below their *leucocephalus* grandparents, and eight which equal or exceed their *albifrons* grandparents.

There are doubtless genetic factors concerned here which influence the degree of saturation of pelage colour, independently of its shade. Of this further evidence will be offered below. Likewise, the fraction

[1] The weighted mean of the F_1 parents of the F_2 generation is 33·97.

$\frac{R-V}{R}$ seems to be the only means at hand of expressing these differences in degree. But the value of this fraction appears to depend upon such a variety of unknown factors that little of a definite nature has thus far been learned of its relation to the inheritance of pelage colour. Perhaps the explanation offered in the concluding section (p. 358) for the unexpectedly high number of seemingly pure segregants affords the best clue to this situation.

That the proportion of non-genetic variability is much higher than in the case of the colour characters hitherto considered is evident from a consideration of parent-offspring correlations. The weighted mean for the *leucocephalus-albifrons* series (pure races and hybrids, excluding F_2–F_3) is $+ 0{\cdot}094$; that for the F_2–F_3 coefficients being $+ 0{\cdot}381$.

Segregants showing aggregate "pure-race" pelage characters. It has been shown for each of the pigmental "characters" thus far considered that a certain number of individuals, in the various segregating generations of hybrids, reach or surpass the degree of depigmentation found in their own *leucocephalus* ancestors. Thus far, one "character" at a time has been considered. It is of interest now to enquire how many individuals in each hybrid generation reach or surpass the mean of one or the other parent race in respect to the entire complex of pigmental characters. In other words, what proportion, if any, of our segregants may be fairly classed as average *leucocephalus* or *albifrons* in respect to coloration[1]?

For this purpose, it would obviously be improper to include as "average" only those individuals which reach or surpass the parental mean value for every one of the characters. For such a standard would exclude all but a small proportion of individuals in a stock of the pure race itself[2]. Accordingly, in considering *leucocephalus* segregants, a limiting value was chosen for each character such that 4/5 of the parent stock of this race would be included. In the case of *albifrons*, the limiting value for each character was such that 5/6 of the parent stock would be included. The reasons for this procedure are as follows.

[1] The fact that thirteen and eleven F_2 individuals, respectively, out of seventy-four (18 and 15 per cent.) fall within the extreme limits of *leucocephalus* and *albifrons*, in respect to all of the pigmental characters, is of little significance in view of the fact that even in the F_1 generation 16 and 7 per cent., respectively, fall within these limits.

[2] Thus, if half of the individuals of a race exceed the mean in respect to character A, only a fourth will exceed the mean in respect to both A and B (supposing that the two are not correlated); only an eighth in respect to A, B and C, etc. Correlation will increase these probabilities somewhat, of course, but the correlations here considered are not as a rule high within the pure races.

In *leucocephalus*, individual differences have been recorded for only three pigmental characters, coloured area, red and the index of saturation $\left(\frac{R-V}{R}\right)$. The other two pigmental characters considered in the present paper (foot pigmentation and tail stripe) are not here included, since their value in *leucocephalus*, with insignificant exceptions, is 0. Likewise the fraction $\frac{A}{R}$ is excluded, since it does not represent a character independent of the first two named above. If we were considering three uncorrelated characters, it is evident that the proportion of a *leucocephalus* population which would be included in the upper (or lower)[1] 4/5 in respect to all of these characters at once would be $(4/5)^3$, or about 51 per cent. Actually, it was found that 34 (54 per cent.) of the sixty-three skins comprising the parent stock of *leucocephalus* fell within the limits set. This agreement is closer than would have been expected, considering that the three characters are all correlated with one another.

In the case of *albifrons*, one further character (tail stripe) has been added to those considered for *leucocephalus*[2]. I have therefore adopted as a limiting value for each of these characters a value such that 5/6 of the *albifrons* population would fall within this limit. Thus, if the four characters were uncorrelated $(5/6)^4$, or about 48 per cent., would fall within this limit with respect to all four. In reality, eighteen out of thirty-nine East Pass *albifrons*, or about 46 per cent., conform to this standard.

Turning to our hybrid population, we do not find a single individual among the seventy-four comprised in the F_2 generation of the *leucocephalus*-East Pass cross which falls within the limits here adopted, in respect to all of the pigmental characters. Four F_2 individuals, to be sure, fall within these limits in respect to all of the values (including also tail stripe and foot pigmentation) except the index of saturation $\left(\frac{R-V}{R}\right)$. But all of these skins are of a richer colour than any but the upper fifth of the pure *leucocephalus* stock (here excluded). This in spite of the fact that a considerable number of other F_2 pelages (twenty among seventy-four) give values of $\frac{R-V}{R}$ which fall within the four-fifths limit for *leucocephalus*.

In the back-cross with *leucocephalus*, we have five individuals out of

[1] Upper or lower, depending on the character. The 4/5 which vary in the direction *away from albifrons* is here intended.

[2] Foot pigmentation has not been included here, since the great majority of East Pass *albifrons* agree with *leucocephalus* in showing a 0 grade for this character. Certain hybrids, nevertheless, exhibit a low degree of foot pigmentation.

fifty-eight which conform to the standards that have been set for an "average" *leucocephalus*. Eight other individuals would have been included except for the excessive value for $\frac{R-V}{R}$. Here, again, it must be pointed out that there is no lack of individuals in this series (there are twenty-one out of fifty-eight) which fall within the limits set for this character.

Among the grades, nine out of forty-one animals measure up to the required standards for all of these characters. Of the twenty-two which fall within the limits in respect to coloured area, only five fail to do so with respect to red, while eleven fail to do so with respect to the index of saturation. This in spite of the fact that nearly 60 per cent. of this entire lot of animals fall within the limits with respect to the latter character.

I have likewise looked into the number of possible *albifrons* segregants in the F_2 generation[1], as judged by the standard referred to above. There is not one individual among the seventy-four which falls within the limits set in respect to all of the pigmented characters, although six of them would do so except for their giving too low values for the index of saturation.

To sum up the preceding enumeration, there is not a single individual, in an F_2 population of seventy-four, which measures up to the standards set either for an average leucocephalus *or an average* albifrons, *in respect to aggregate pigmental characters. In the first back-cross with* leucocephalus, *five individuals showing average characters for the latter race appeared in a population of fifty-eight. In the second back-cross ("grades"), there are nine cases in a population of forty-one.*

It must not, of course, be supposed that such an enumeration as the foregoing reveals the exact number of segregants which are pure for all *leucocephalus* colour factors. It merely gives an approximate answer to the question: How many individuals are there in which segregation is so nearly complete that they equal or surpass[2] the average *leucocephalus* phenotypically?

One circumstance which was noticed during the life of the animals is reflected in the figures which have here been considered. This is the fact that most of the paler variants among the F_2 and back-cross generations (including grades) are of a distinctly richer colour than *leucocephalus*, with which they would otherwise be closely comparable. That this is not

[1] The number of offspring derived from back-crosses with *albifrons* is too small to be considered here.

[2] *I.e.* surpass it in the direction away from *albifrons*.

due to any lack of segregants having a low index of saturation has already been pointed out[1]. It is due to the complete absence, in these hybrid generations, of any positive correlation between pallor and low saturation, such as obtains in *leucocephalus*. Quite the contrary, we meet with a positive correlation between pale shade and *rich* colour in both the F_1 and F_2 generations of this cross.

The question naturally arises whether the *leucocephalus*-like derivatives of the *leucocephalus-albifrons* cross agree with the former race in characters other than pigmentation. The other racial differences upon which stress has chiefly been laid are length of tail and foot. But these differences concern mean values only. The distribution frequencies for both characters overlap broadly in the two races. No such detailed analysis of these values seems desirable here as was presented in the case of colour characters. It need only be stated that the five back-cross individuals above referred to, as well as the nine among the grades, fall within the range of *leucocephalus* with respect to both tail and foot length, while in an actual majority of these cases the measurements of tail and foot equal or exceed the mean values for these members in *leucocephalus*.

Correlations. Considerable attention has been devoted to correlations between the various characters thus far discussed. Table V presents such coefficients as have been determined for the parent stocks and for the various crosses. Correlations between various characters and size (body length) have likewise been computed, though they are not here included. The latter render possible the computation of "corrected" values for various characters which are strongly influenced by size.

The facts revealed by the correlation coefficients and graphs (Text-figs. 8, 9, 10), so far as the *leucocephalus-albifrons* (East Pass) cross is concerned, may be summarised as follows:

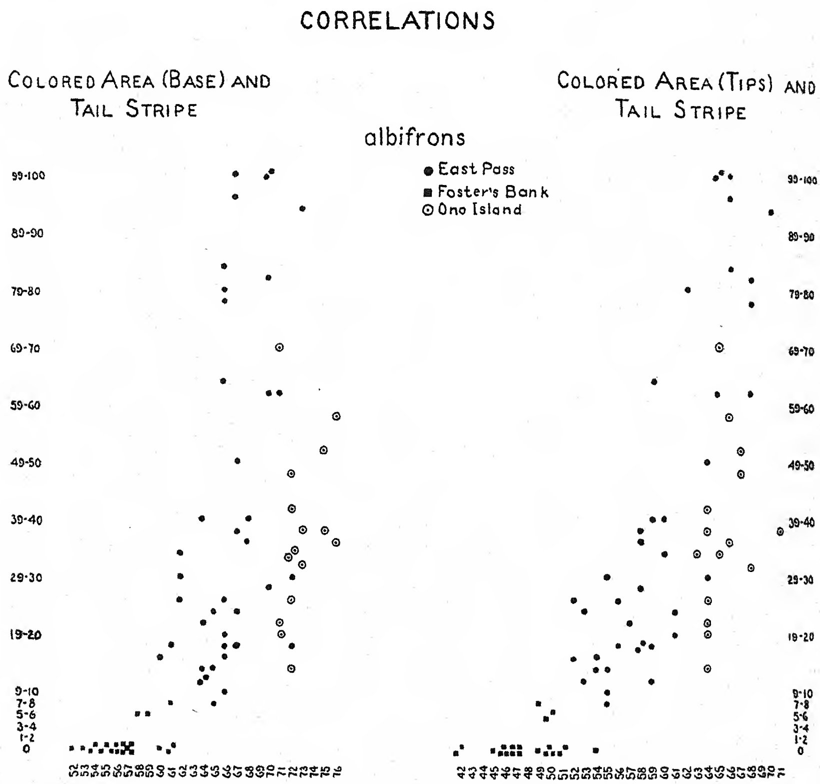
(1) All linear measurements (tail, foot, ear, pelvis, femur, skull length, skull breadth), as well as weight, show, as might have been anticipated, rather high positive correlations with body length in nearly all of the populations here considered. In general, there are no differences of interest, in the magnitude of these correlations, between the various races or generations of hybrids or between the sexes[2].

[1] Nor is it probably due to any effects of captivity. The mean index of the C_1 *leucocephalus* is slightly *lower* than that of the "wild" generation of *leucocephalus*, though slightly higher than the weighted mean of their own parents.

[2] There is a moderately strong probability of a correlation between body length and the number of caudal vertebrae, when both the *leucocephalus-albifrons* and the *leucocephalus-polionotus* series are considered. There are eleven positive coefficients out of

(2) There are no constant correlations between body length and any of the pigmental characters. Occasional single figures are of moderate statistical significance, but the relations shown by the various series are so contradictory that the existence of any true correlation is doubtful.

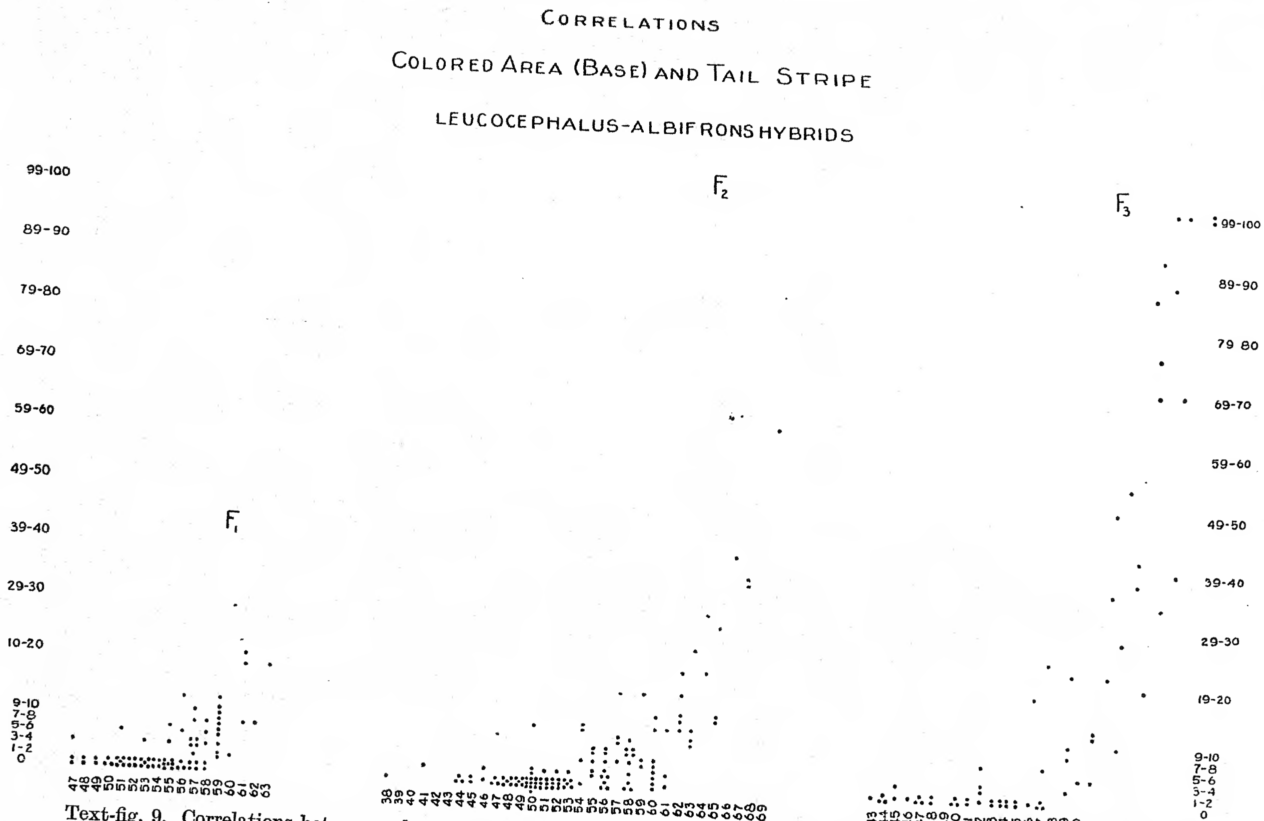
As regards the correlations between various characters, other than body length, I have restricted the computations mainly to characters which differ in the races that have been crossed.



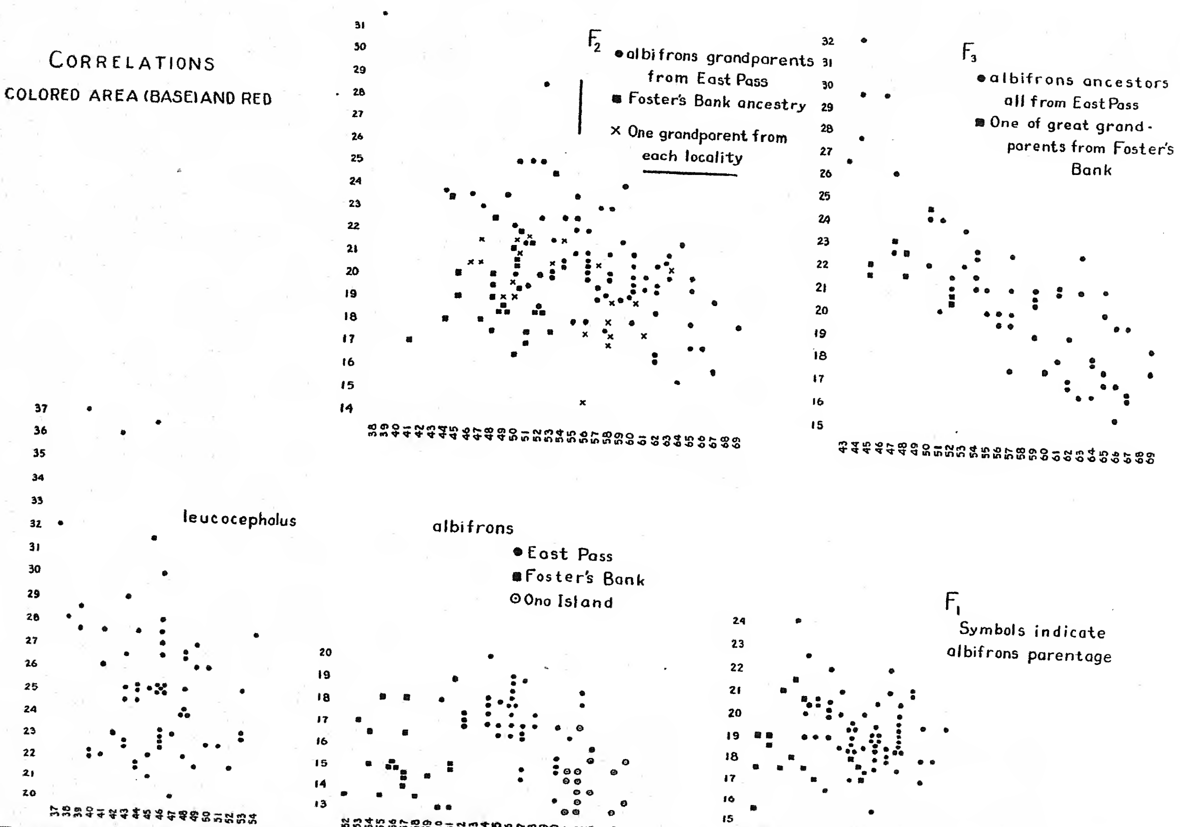
Text-fig. 8. Correlations between coloured area of pelage (abscissas) and tail stripe (ordinates) in *albifrons* (the three local collections being distinguished).

(3) An undoubted positive correlation exists between the length of the tail and foot. This is true not only of the "gross" but of the "net" correlation, *i.e.* that which remains when the influence of general body-

fourteen (the fourteen groups being the males and females of the three pure races and of the F_1 and F_2 generations of two crosses), while the weighted mean of the fourteen coefficients (based on 454 individuals) is $+0{\cdot}142$.



Text-fig. 9. Correlations between coloured area and tail stripe in three generations of *leucocephalus-albifrons* hybrids.



Text-fig. 10. Correlations between coloured area (abscissas) and red (ordinates) in *leucocephalus*, *albifrons*, and three generations of hybrids. The influence of the different *albifrons* stocks is evident, even in the F_3 generation.

size has been eliminated[1]. Wide differences are found in the magnitude of this coefficient, according to the race, generation or sex comprised in the group under consideration. But none of these differences have any evident biological interest. Low positive correlations likewise exist in all cases between tail and ear length and in most cases between ear and foot, even when the influence of body size has been removed.

(4) Significant correlations exist, in many cases, among the various pigmental characters. These correlations are positive between tail stripe and coloured area; negative between the former and red; negative between red and coloured area.

(5) Despite single instances, no consistent correlations exist between tail length and any of the pigmental characters. As regards foot length the case appears to be different. Out of thirty-eight coefficients which have been computed for *leucocephalus*, *albifrons* and the five series of hybrids involving these two sub-species, twenty-four are of the sign which would be expected on the supposition that racial peculiarities in respect to pigmentation and foot length are genetically associated. When we consider these series of animals separately, moreover, we find that the preponderance of "expected" signs is due entirely to the F_2 and F_3 generations of hybrids, for which the twelve coefficients are all consistent with the foregoing interpretation. These are of course the generations in which such a genetic association of racial characters would be most evident. The testimony of these figures is not altogether cumulative, to be sure, since the various pigmental characters are all correlated with one another. But taken in connection with the even stronger evidence from the *leucocephalus-polionotus* cross, it can hardly be regarded as due to random sampling. These facts will be discussed more fully in relation to the cross next to be considered.

(6) The correlations within the single groups, which have been recorded under (4) and (5), correspond exactly to the manner in which the respective races differ from one another. Thus, *leucocephalus*, *albifrons* and *polionotus* form a series of increasing depth of shade (decreasing value of "red"), and also a series of *increasing* value of coloured area, tail stripe and foot pigmentation[2]. Likewise, *leucocephalus* differs from *albifrons* in having a significantly greater foot length.

(7) These correlations, for the most part, are greater in the F_2 than

[1] I have called attention to this correlation in several previous papers.

[2] In recent papers (1929, 1929 *a*), I have shown that these same inter-racial correlations in pigmental characters held when we made a series of collections along a geographic gradient, through the range of *albifrons* into that of *polionotus*.

in the F_1 generation. In the majority of cases, they are largest of all in the F_3 generation, derived from selected F_2 parents (p. 282). Thus the correlation between coloured area and red is -0.326 in the F_1, rising to -0.682 in the F_2 and -0.788 in the F_3. It is significant, though of moderate magnitude, in both *leucocephalus* and *albifrons*.

(8) Correlations between the index of saturation $\frac{R-V}{R}$ and the other pigmental characters are less easy to generalise. In *leucocephalus*, the correlation with red is negative, but in *albifrons* it is strongly positive, as is the case with the F_1, F_2 and F_3 generations of hybrids. In the back-crosses (3/4 *leucocephalus*), on the other hand, the coefficient is practically 0, while in the grades (7/8 *leucocephalus*) it is negative. Thus, with an increasing proportion of *leucocephalus* "blood," we have an approach to the relation found in the latter race[1]. Correlations between this index and coloured area have, in general, an opposite sign to correlations with red, though this is not true in all cases. It must be repeated that the genetic relations of this character are more obscure than those of the other pigmental characters here discussed.

The facts considered under (6) and (7) make it plain that the various colour characters therein considered are either manifestations of identical genetic factors, or at least are dependent upon closely linked factors. This subject will be discussed after the other crosses have been considered.

Regarding the correlations between length of tail stripe and other pigmental characters, it must be said that the calculation of coefficients, according to the customary procedure, is not strictly legitimate, owing to the extreme asymmetry of the distributions (Text-fig. 2). The reality and magnitude of these correlations will, however, be realised by reference to Text-figs. 8 and 9. An interesting example of this intimate relation between the extent of the coloured area and the degree of development of the tail stripe is found in plotting the correlation between the values of coloured area in the *leucocephalus* parents and of tail stripe length in their F_1 offspring (Text-fig. 3). A distinct positive correlation seems to be manifested, despite the fact that the tail stripe is always wholly lacking in *leucocephalus*[2].

[1] The negative correlation in *leucocephalus* is probably due, in part at least, to a detail of procedure. Pelages in which the dorsal coloured area is small allow of the inclusion of considerable margins of the whitish lateral region within the rectangular area from which the instrumental reading is taken. The latter is of constant size for all pelages.

[2] This relation is even better shown in the *leucocephalus-polionotus* cross, next to be considered.

(*b*) *The* leucocephalus-polionotus *series.*

(Text-figs. 11–24; Plates VIII, IX, XI.)

Tables II and IV give the mean values and standard deviations for the parent races and hybrid generations here concerned. As already implied in the preliminary account of these sub-species (pp. 279–81), *polionotus* differs much more widely from *leucocephalus* than does *albifrons*. There are significant differences in both tail length and foot length, the latter being particularly striking in proportion to the variability of this member. There is, however, a considerable amount of overlapping in the frequency polygons for tail length in the two races, though this is almost entirely lacking in the case of foot length, at least when corrected values are considered. As regards degree of pigmentation, on the other hand, none of the measured characters based upon this show any overlapping whatever. In other words, the palest *polionotus* is more deeply and extensively pigmented than is the darkest *leucocephalus*. This is well shown in the graphs (Text-figs. 14, 17, 18). There are also certain differences which are absolute ones rather than differences of degree. Thus in *polionotus* (at least in the population here considered) the tail stripe invariably extends from base to tip, and is otherwise well developed, while the soles of the feet of the great majority of individuals are more or less heavily pigmented. In *leucocephalus*, both tail stripe and foot pigmentation are entirely lacking[1]. Likewise, in *polionotus*, the ventral and lateral parts of the pelage consist of hairs which are pigmented throughout the basal half or more of their extent, while in *leucocephalus* the hairs of most of this area of the body are entirely white.

Hence more of interest might reasonably be expected from the cross between *leucocephalus* and *polionotus* than from that between *leucocephalus* and *albifrons*. We may add to this the fact that there are larger numbers of comparable individuals in the present series, since the *polionotus* stock was obtained in one locality, and there is thus no necessity for subdividing the hybrid generations according to ancestry. The various measured characters will now be considered in order, as before.

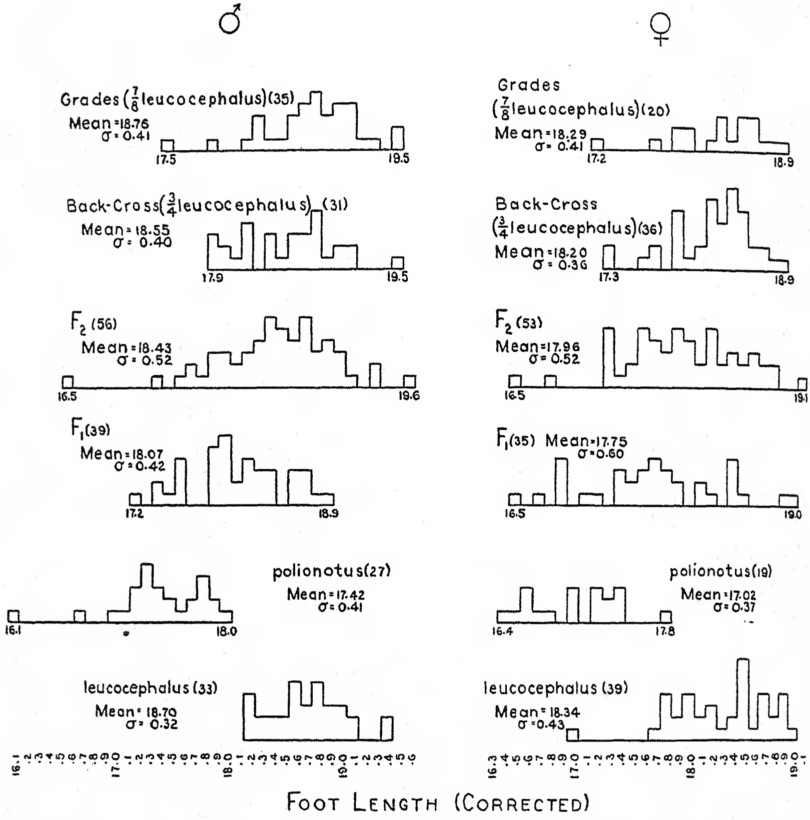
Body length and *weight*. Here, as before, there are probably no significant differences between the two sub-species in size. Nor is there any real evidence of heterosis in the F_1 hybrids.

Tail length. As before stated, this appendage is longer in *leuco-*

[1] In a few C_1 individuals faint traces are recorded, but this may be due to my having adopted a slightly more exacting standard for the 0 grade in my later determinations.

cephalus, the mean difference being nearly 3 mm. The condition in both hybrid generations is intermediate.

Foot length. This, as above stated, is distinctly greater in *leucocephalus*, the mean difference being about 1·2 mm. Here again, the first and second hybrid generations are intermediate, though the males of the F_2 generation for some reason show an appreciably greater foot



Text-fig. 11. Length of foot in *leucocephalus*, *polionotus* and hybrids. The values for this character have been corrected for a standard body length of 80 mm. Males and females are dealt with separately, owing to marked sexual differences.

length than those of the F_1 (Text-fig. 11). As regards the relative variability of these two generations, the two sexes show opposite relations, the standard deviation for the females being lower in the second than the first. Capricious results are not surprising in the case of foot length, in view of the sensitiveness of this member to nutritional and other environmental conditions, and to the large proportion of non-

genetic variability, as shown by parent-offspring correlations. The weighted mean of the correlations between the parent and C_1 generations of *leucocephalus* and of *polionotus*, and those between the F_1 and F_2 generations of hybrids, based upon more than 200 offspring, is + 0·148[1]. The corresponding figure for coloured area is + 0·384.

The successive back-crosses with *leucocephalus*, as might have been expected, show an approach to the greater foot length of the latter sub-species.

Ear length. This is slightly greater in *polionotus* and the difference is perhaps significant. In the males, though not in the females, the condition is intermediate in both F_1 and F_2 generations. The standard deviation, in each sex, is larger in the F_2 generation, though in neither case is the difference significant.

Considering the *skeletal characters*, *polionotus* gives a slightly higher average number of caudal vertebrae than *leucocephalus*, and in both sexes a slightly longer pelvis, but shorter femur and shorter skull. Some of these differences have a fairly high statistical significance, and thus may represent actual differences between the races concerned. As regards the relative variability in the two hybrid generations, we find no general consistency, the sexes, in some cases, giving contradictory results.

Reviewing these six linear measurements (tail, foot, ear, pelvis, femur, skull length), and considering the sexes separately, we find that in nine cases the F_2 generation presents a higher standard deviation, and in three cases a lower one. This preponderant increase in variability may possibly be due to the segregation of multiple size factors, or it may be purely accidental.

Of far greater interest are the pigmental characters, in respect to which the sub-specific differences are much more pronounced.

Tail stripe length. As already stated, all specimens of *polionotus* here considered give a 100 per cent. value for this character, while all specimens of *leucocephalus* give a 0 value. As in the case of the *leucocephalus-albifrons* cross, we have a partial dominance of the stripeless condition, the mean in the F_1 generation being 18·29, instead of 50. Likewise, we have, as in the latter cross, a decided increase in the mean value in the F_2 generation (26·05), as compared with the F_1, *i.e.* a shifting of the mean in the direction of the recessive character. That this higher value in the F_2 generation is not due to any accidental choice of F_1 parents having more fully developed tail stripes is shown by the fact that

[1] For reasons which need not be discussed here, comparison is restricted to these generations.

these F_1 parents give a weighted mean of 18·81, which is fairly close to that of the F_1 generation as a whole.

It is, as previously stated, hardly legitimate to compute standard deviations for a character with such asymmetrical distribution. These figures are, nevertheless, given in the tables. But it is much more profitable to compare graphically the behaviour of this character in the various hybrid generations (Text-fig. 12). In both the F_1 and F_2 we have values ranging from 0 to 100. But whereas in the F_1 the percentage of extreme cases (0 and 100) is in each instance 5·2, in the F_2 the percentage of these extremes is 11 and 12·8 respectively. There is, furthermore, a considerable increase in the proportion of the larger values in the F_2 generation, a fact which is responsible for the higher mean.

Back-crosses with *leucocephalus* give a mean value of 2·04, while 55 per cent. are of the 0 grade, and the highest value is 13. In the small group of back-crosses between F_1 hybrids and *polionotus*, the mean is 45·19, while none reach the 0 grade, and three reach the grade of 100.

In the group of grades (7/8 *leucocephalus*), the mean is 1·49, while 71 per cent. are of the 0 grade. In this case, the highest single value is 14, which is slightly higher than that in the first (3/4) back-cross.

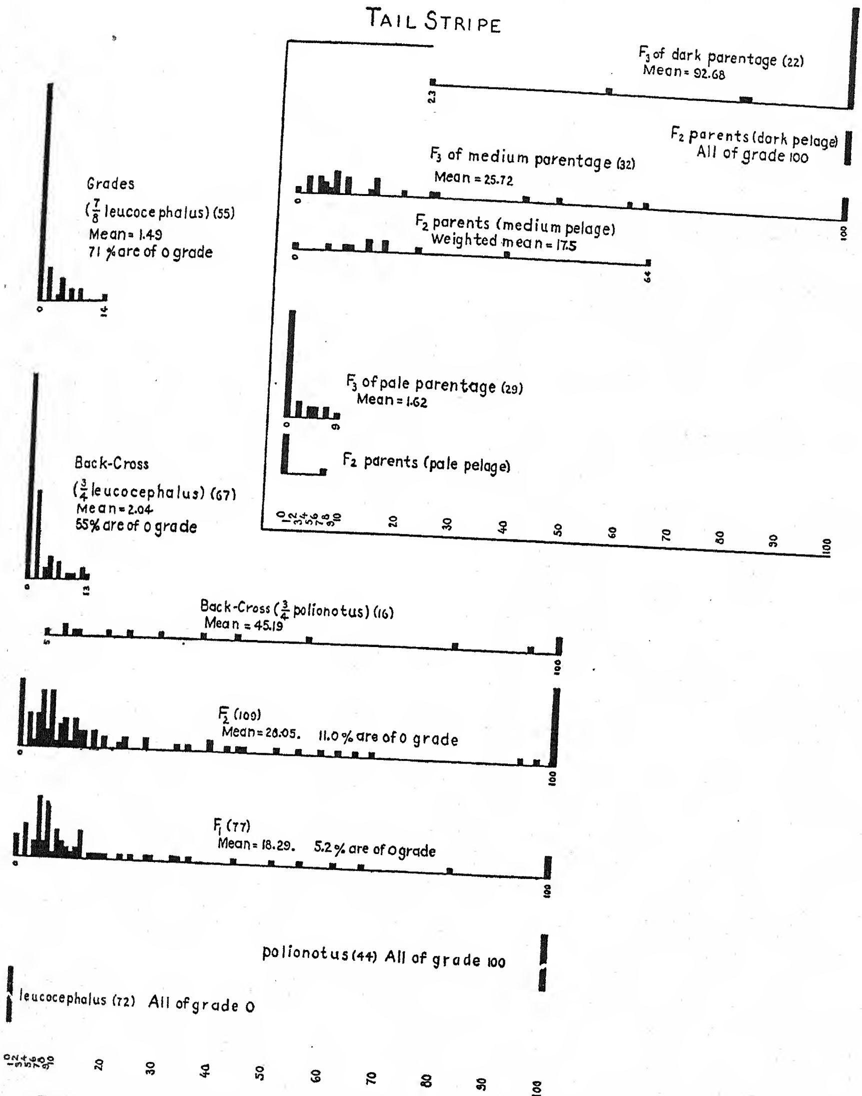
In successive crosses with *leucocephalus* there is no consistency in the degree of dominance of the stripeless condition over its presence, complete or partial.

It has been seen that the hybrids between *polionotus* and *leucocephalus* agree with the "pure" race *albifrons* in possessing a commonly incomplete as well as a highly variable tail stripe. In the former case, as in the latter, it is a matter of interest to determine to what extent, if any, these individual differences are hereditary.

Considering first the F_1 generation, we cannot of course correlate differences of tail stripe here with corresponding differences in their parents, since, in every case, one parent possesses a complete stripe, while the other lacks it altogether. But we obtain highly interesting correlations between the magnitude of the coloured area in the parents of each race and that of the tail stripe in the hybrid offspring (Text-fig. 13)[1]. It is of interest that a higher correlation is shown here with the *leucocephalus* parents than with the *polionotus* ones, although the former race lacks the tail stripe altogether. These relations furnish additional evidence for the common genetic basis (or at least close linkage) of tail stripe and coloured area (see p. 291).

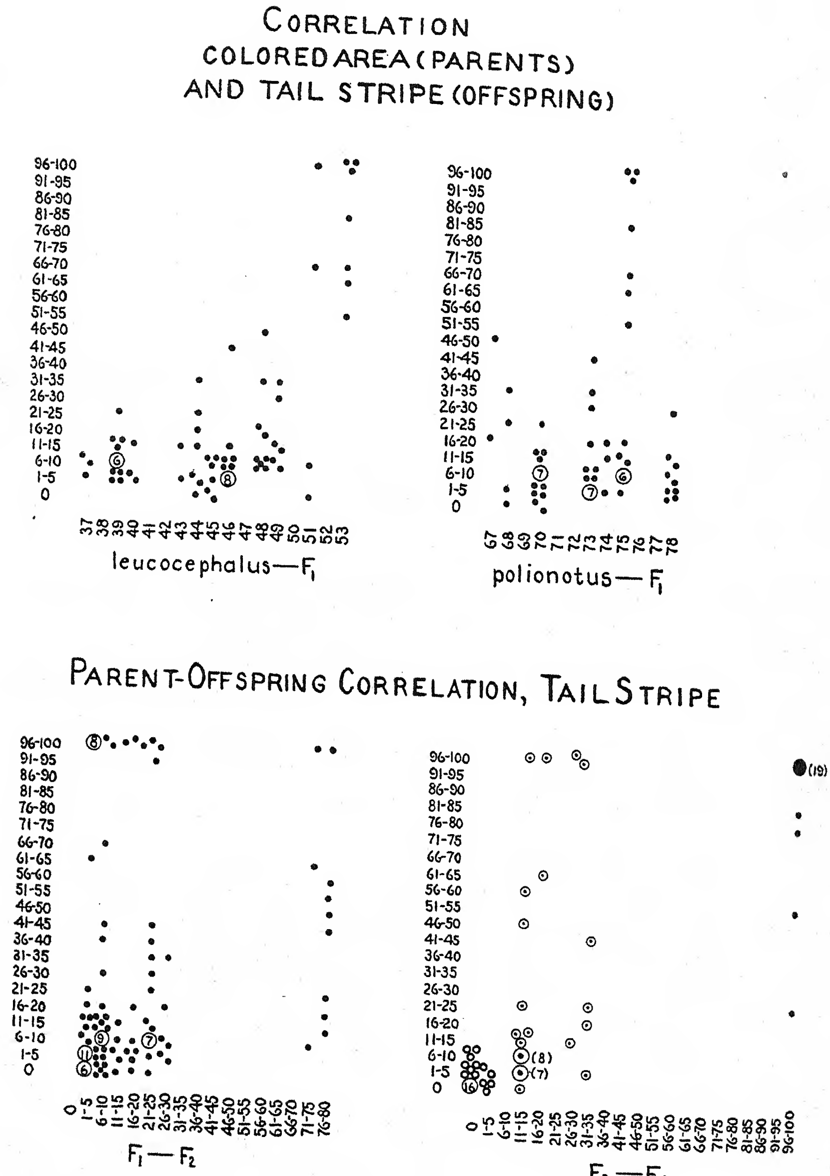
[1] Coefficients of parent-offspring correlation cannot profitably be computed for tail stripe length, for reasons already indicated.

Correlation between the magnitude of the tail stripe in the F_1 and the F_2 generations is largely concealed by the high degree of genetic



Text-fig. 12. Genetic behaviour of tail stripe in the *leucocephalus-polionotus* cross.

segregation in the latter generation (Text-fig. 13). But such correlation is strikingly shown between the selected F_2 parents and their F_3 off-



Text-fig. 13. Correlations between tail stripe (parents) and tail stripe (offspring), and between coloured area (parents) and tail stripe (offspring), in the *leucocephalus-polionotus* cross. The symbols employed for the F_2–F_3 series denote offspring of the "pale," "medium" and "dark" groups of selected F_2 parents respectively (see Text-fig. 20). Of greatest interest is the undoubted correlation between the coloured area of both parent races, particularly *leucocephalus*, and the tail stripe of the F_1 offspring. This despite the total lack of tail stripe in *leucocephalus*.

spring[1]. The mean values of tail stripe length for the "pale," "medium" and "dark" groups are 1·6, 25·7 and 92·7 respectively. The weighted means of the F_2 parents of these groups are 0·6, 17·5 and 100 respectively (Text-fig. 12).

It is interesting that the high correlation between these two generations is due chiefly to the presence of the "dark" and "pale" groups. Within the largely heterozygous "medium" group, little or no parent-offspring correlation is to be detected, just as was the case when we dealt with the offspring of the F_1 generation. It is thus plain that the "pale" and "dark" groups, both in the F_2 and F_3 generations, represent stocks which differ rather widely from one another genetically. They result from a partial segregation, in the gamete formation of the F_1 generation, of colour factors derived from *leucocephalus* and *polionotus* respectively.

It should be evident by this time that the differences between average members of any two of our races are wholly genetic, while differences among individuals of the same race are only partly genetic, and in some cases may be preponderantly non-genetic.

Foot pigmentation. The mean value of this character for the parent generation of *polionotus* is 1·47, that for *leucocephalus* being 0. The figures for the F_1 and F_2 generations are 1·06 and 0·83, respectively, both of these being above the mean for the parent races. The successive back-crosses give 0·48 and 0·31 respectively[2]. The variability of the F_1 and F_2 generations is nearly equal.

That individual differences in the degree of foot pigmentation are in part genetic has been shown for other species (Sumner, 1923*a*; Sumner and Huestis, 1925). In the present case, the weighted mean of the coefficients of parent-offspring correlation for pure *polionotus* and for the successive generations of *leucocephalus-polionotus* hybrids is + 0·295.

Coloured area of the pelage. It is impossible to make an exact comparison between the mean values of the parent races for coloured area, since different measurements have been taken in the two cases. The

[1] See p. 291. It is probable that in this case the extent of the tail stripe was one of the factors which influenced my selection of the individuals as "pale," "medium" or "dark." This circumstance would of course tend to increase the correlation.

[2] It is questionable whether there is any dominance here of the more highly pigmented condition. There are reasons for believing either that the degree of foot pigmentation is somewhat affected by the conditions of captivity or that a slightly different standard was employed with the later series of animals than with the original stocks. Thus, the C_1 generation of *P. p. polionotus* gives a mean value of 1·97. All of the sub-species of *Peromyscus polionotus* have relatively low grades of foot pigmentation, as compared with *P. maniculatus*, and the task of grading is correspondingly difficult.

only one which can be determined accurately in the case of *leucocephalus* is the area of hairs pigmented at the base (A_b). In *polionotus*, on the other hand, this area would comprise practically the entire pelage. The coloured area of the latter, therefore, is the region of hair which is pigmented to the tips, *i.e.* the area of coloured hair which is visible when the skin is viewed from the outside (A_t). It has seemed desirable, nevertheless, to obtain approximate values for A_t in *leucocephalus* and A_b in *polionotus* in order to render possible crude comparisons between these two races. Ten skins of the former sub-species (five of each sex) gave a mean value for A_t of 33·6; ten skins of the latter a mean value for A_b of 93·3.

For the F_1 and F_2 generations of hybrids both of these measurements were made. In the case of the back-crosses and grades, however, A_b only was determined as in *leucocephalus*.

The mean values and standard deviations for these measurements in the F_1 and F_2 generations are as follows:

	A_b		A_t	
	Mean	σ	Mean	σ
F_1	68·33	6·46	54·46	4·89
F_2	69·12	13·87	54·34	9·02

Thus, while the mean values in these two generations agree fairly closely, there is a very great increase of variability in the second hybrid generation.

Text-fig. 14, which gives the distributions of A_b and A_t for the parent races and certain hybrid generations, reveals in a striking way the extent of this increased "spread" in the F_2 generation, as well as various other features of interest. It will be seen that whereas no single F_1 individual falls within the range of *leucocephalus* for A_b, sixteen individuals, or about 15 per cent. of the F_2 generation, fall within these limits. Of these, two individuals fall below the mean value for *leucocephalus*.

At the opposite extreme, there are no individuals which reach the approximate mean (93) which was derived from the measurement of ten *polionotus* skins (see above), although there is a considerable group which approach this value. There results from this last circumstance a distinct bimodal appearance in our frequency polygon, with a secondary mode not far below the *polionotus* mean. That this appearance is not, however, due to any simple segregation, relating to a single pair of allelomorphs, is probable from the following considerations. (1) These exceptionally high values are due to the presence of basally pigmented hairs throughout virtually the whole of the ventral pelage, as in *polionotus*. In many other pelages pigmentation is likewise present in the

ventral hair, but it is so faint as to be invisible or nearly so when the skin is viewed by transmitted light and measured with a planimeter. Only when this pigmentation becomes very distinct is it comprised within the A_b, as here measured, and in such cases the entire area, to the periphery of the skin, is commonly included; hence the relative discontinuity in the distribution of values. On the other hand, even in the individuals comprised in this secondary mode, the pigmentation is usually less intense than in that of most *polionotus*[1]. (2) When we take the other measurement of coloured area, A_t (Text-fig. 14, upper part), we find no such appearance of a bimodal distribution. Yet these two characters are closely correlated (+ 0·891, in the F_2), and probably depend to a large extent upon identical factors.

From the figure it appears that three individuals of the back-cross with *leucocephalus* fall below the mean of the latter race for coloured area, while twenty-eight individuals among the grades, or 51 per cent., fall below that mean.

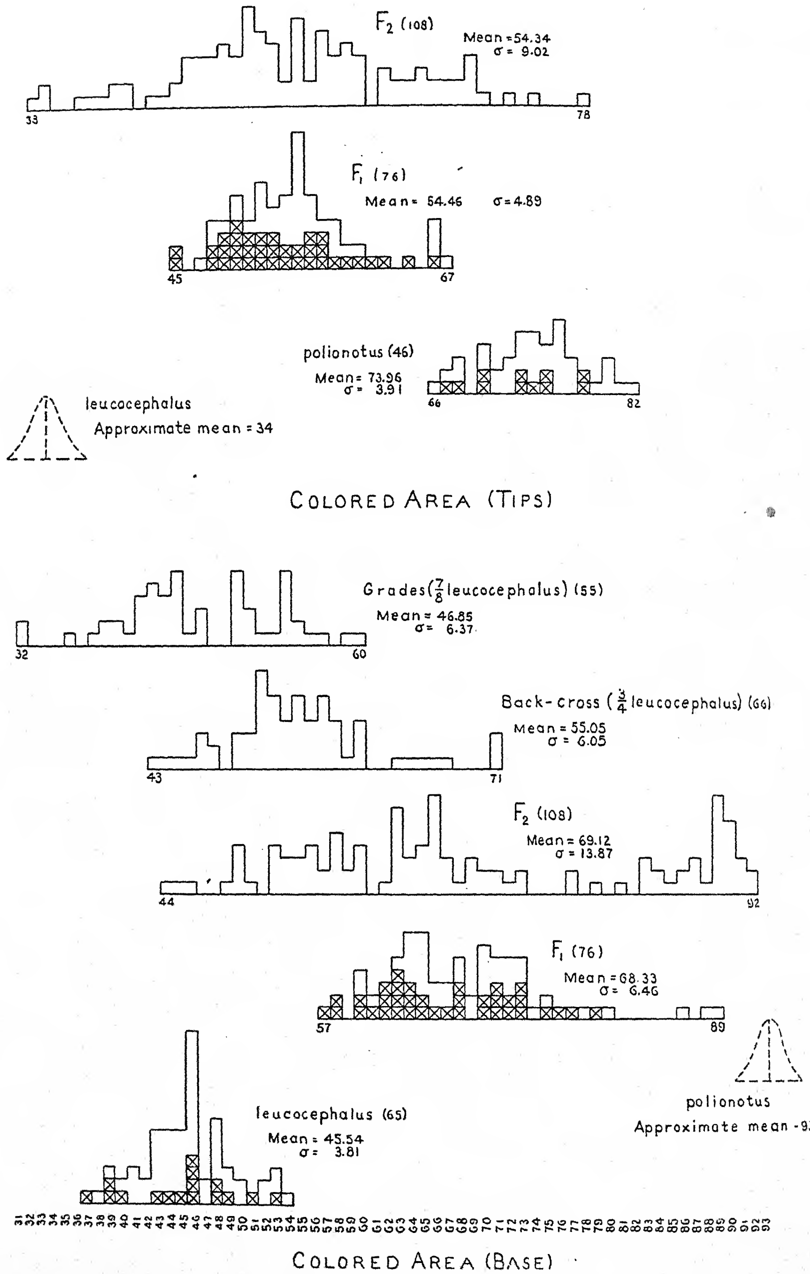
The small group of back-crosses between F_1 and *polionotus* (not figured) give an unexpectedly low value (58·07) for A_t. This might be intelligible if the values of the individual parents were considered.

Considering the graphs for the other measurement of coloured area (A_t), we find five F_1 individuals which fall within the range of *polionotus*, but none which approach at all closely the mean of the latter. In the F_2 generation, however, fourteen individuals, or 13 per cent., fall within the limits of *polionotus*, while two surpass the mean value of the latter. At the opposite extreme three individuals nearly or quite reach the approximate mean which was determined for *leucocephalus*.

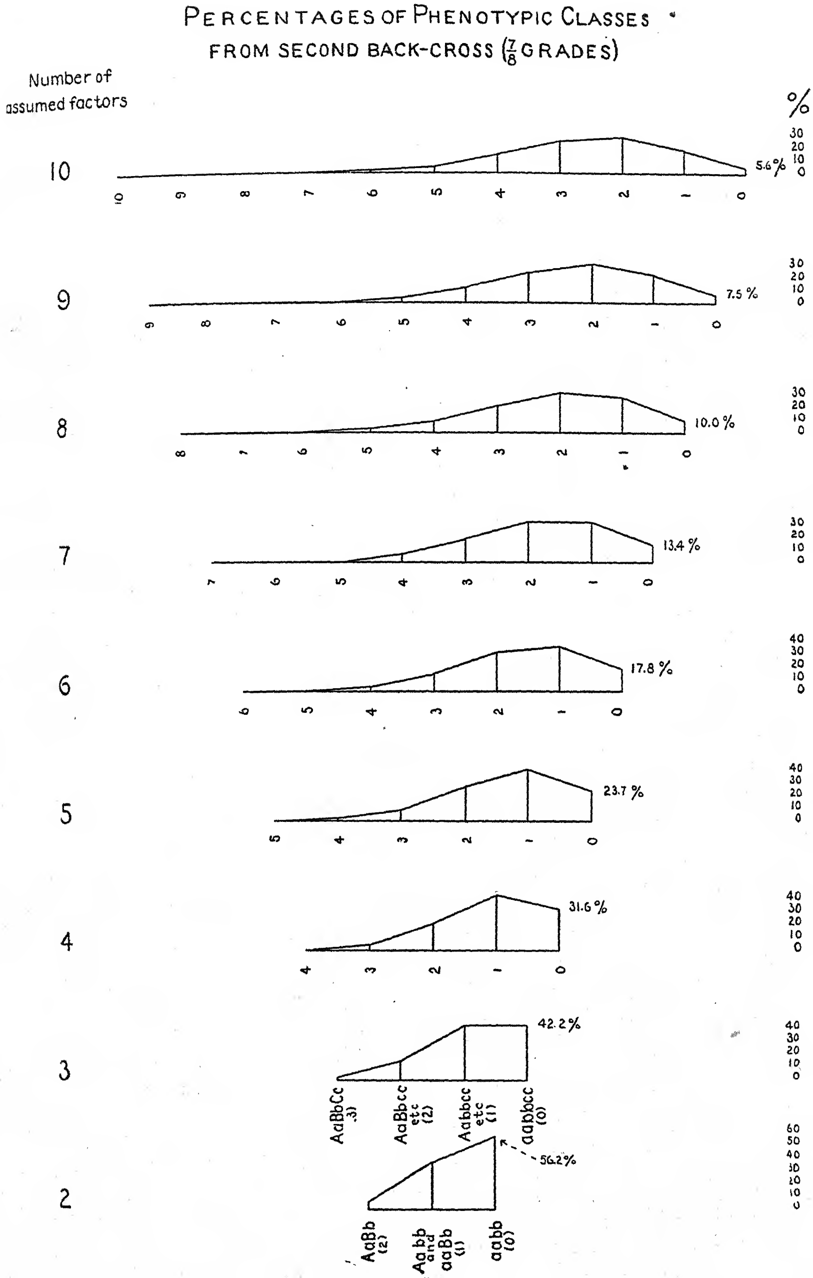
When we compare each individual with its own *leucocephalus* ancestor (or the mean of these, where more than one is concerned), instead of comparing it with the mean for the entire *leucocephalus* population, we have the following situation. In the F_2 generation, we find one individual, out of 108, which gives a value for A_b equal to that of its *leucocephalus* grandparent, and one individual which gives a value for A_t which probably exceeds that of its *polionotus* grandparent[2]. If these

[1] An endeavour to divide the material into classes, with and without an obvious amount of pigment in the ventral hair, proved to be entirely futile. Nor has it proved worth while to grade these pelages according to "pigmentation of ventral hair," as was done for local collections of wild material in a recent paper (Sumner, 1929). Inspection has revealed no instructive relations here.

[2] The pelage of this *polionotus* ancestor is not available, owing to premature death, but the value for this particular F_2 pelage is equal to that of the highest known *polionotus* used for breeding.

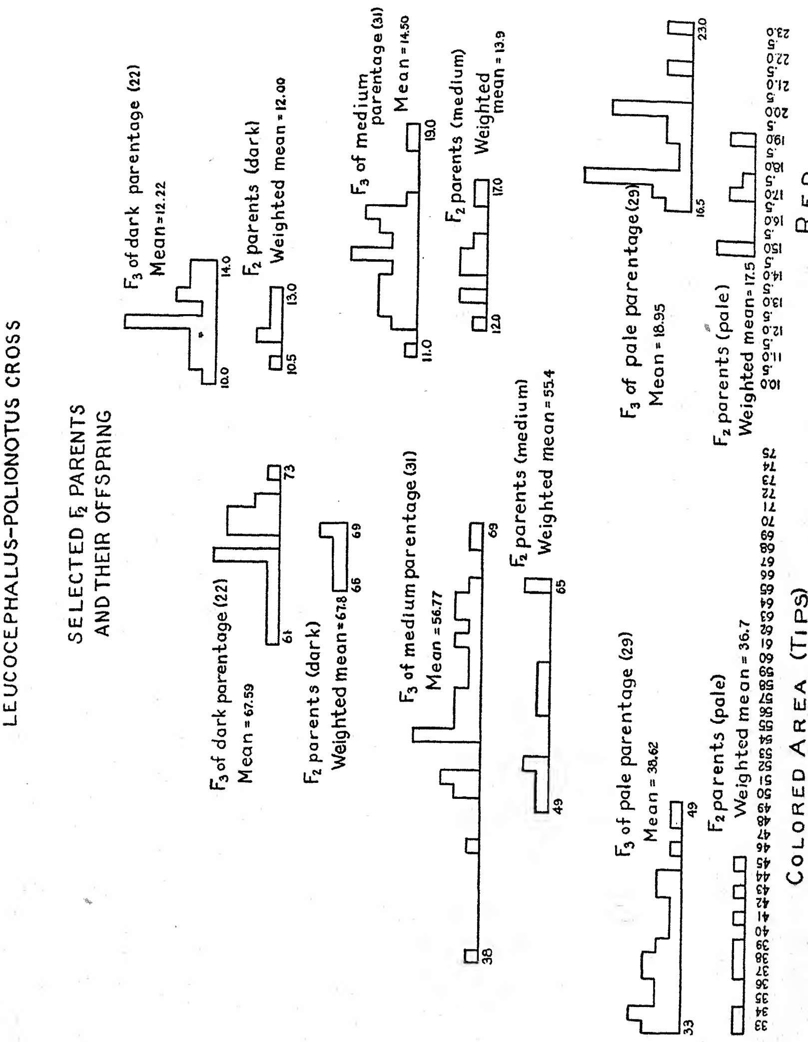


Text-fig. 14. Genetic behaviour of the coloured area of the pelage (both determinations) in the *leucocephalus-polionotus* cross. Parents designated by cross-hatched squares, as before.



Text-fig. 15. Theoretical distributions of the various phenotypic classes in a second back-cross to one of the parent stocks, following a cross between two races (see footnote on p. 296).

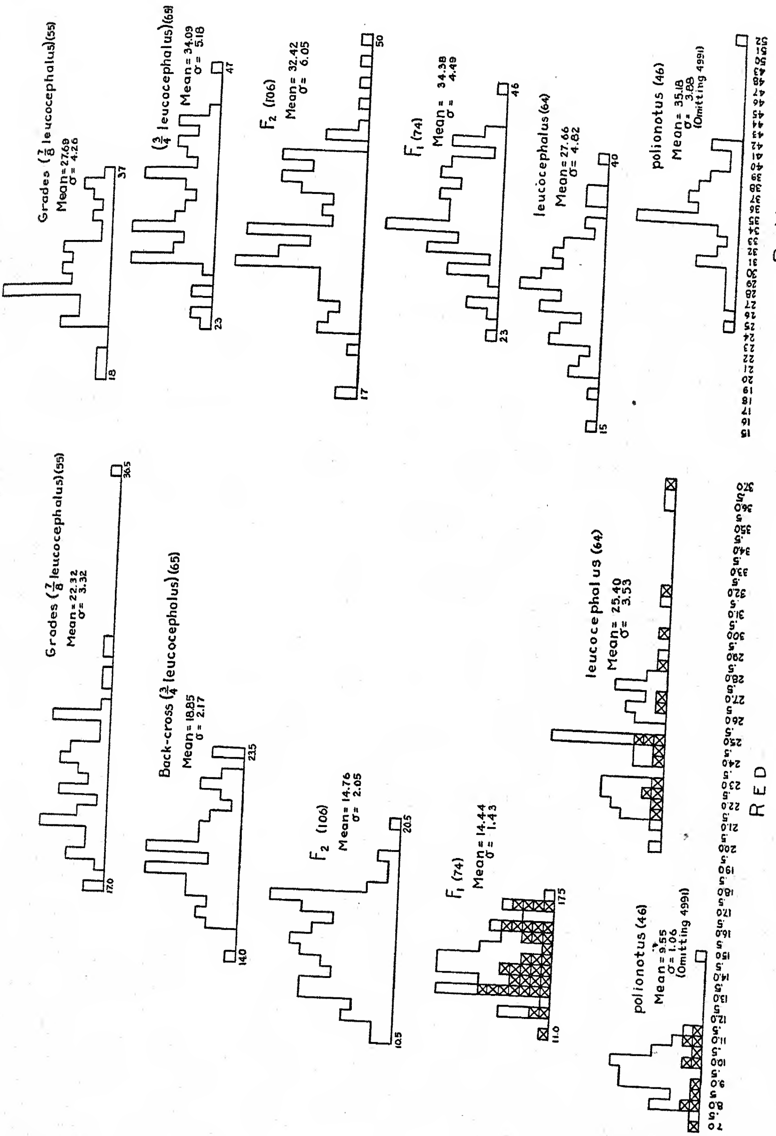
two were regarded as "pure" segregants, the number would be between the expected proportions for three and four factors respectively. Among the back-crosses (3/4 *leucocephalus*) are four out of sixty-six which fall



Text-fig. 16. Two pelage characters in selected F_2 parents and their F_3 offspring (*leucocephalus-polionotus* cross).

below the mean of their own *leucocephalus* ancestors. This is almost exactly the proportion for four factor differences. Finally, among the grades (7/8 *leucocephalus*), we have twenty-four individuals out of fifty-five which equal or fall below their *leucocephalus* ancestors. This is

44 per cent., a value very close to the expected proportion (42·2) for three factors.



Text-fig. 17. Values of red and the index of saturation for the parent races and hybrids of the *leucocephalus-polionotus* cross.

Thus far, the results are reasonably consistent, the indicated number of factors (according to the criterion adopted provisionally) being three or four. On the other hand, little or no tendency is to be noted toward

a massing of the values on the left-hand side of the polygon for the "grades" (Text-fig. 14), as would be expected were so few factors concerned (Text-fig. 15). I shall return to this subject later.

It is desirable, as before, to determine to what extent individual differences in the values for this character are hereditary. The weighted mean of the various coefficients of correlation between the generations of the pure races (*leucocephalus* and *polionotus*), and of the hybrids (exclusive of that between F_2 and F_3) is + 0·294. This is considerably lower than the similar figure for the *leucocephalus-albifrons* series (+ 0·375). The difference is perhaps due to the heterogeneous nature of the *albifrons* stock, included in the earlier computations. On the other hand, the correlation between the selected pairs of F_2 parents and their F_3 offspring is + 0·917.

Graphs showing the distribution of values among these F_3 animals are instructive (Text-fig. 16). Of significance is the much greater range of the "medium" group, as compared with either of the others; also the reversed unilateral arrangement of the other two groups. The first of these relations may be noted in the case of the *leucocephalus-albifrons* cross (Text-fig. 6, coloured area, but not red). It is probably due, at least in part, to the greater heterozygosity of F_2 individuals of intermediate shade, as compared with the more extreme types.

This greater spread of the F_3 "medium" group is even more conspicuous in the case of the A_b values, but the unilateral arrangement of the "pale" and "dark" groups is much less evident (not figured).

Red. It will be seen (Table II and Text-fig. 17) that the mean values for this character are far apart, being 25·4 and 9·55 for *leucocephalus* and *polionotus* respectively. Moreover, the extreme values do not approach one another at all closely, despite the high variability of *leucocephalus*. The mean value in the F_1 generation represents a much darker shade than the mid-point between the parental means, being 14·44 instead of 17·5. There is thus a tendency toward dominance on the part of the *polionotus* factors which control shade. The slight, though perhaps significant, increase in the F_2 mean over the F_1 is in the expected direction (see p. 300)[1].

Of more certain significance is the increase of variability in the F_2 generation as compared with the F_1 (2·05 and 1·43 respectively). In comparison with the *leucocephalus-albifrons* cross, however, this increase

[1] It is possible that some of the differences between successive hybrid generations, in respect to this character, are due to non-genetic agencies. Cage-bred *polionotus* appear to be slightly paler (*i.e.* have a higher mean value for red) than their "wild" parents.

in variability is considerably less evident. Only a single F_2 individual falls within the range of *leucocephalus*, while none even approach the mean value of the latter. On the other hand, nine individuals fall within the range of *polionotus*[1], although none reach the mean of this race.

In the first back-cross generation (3/4 *leucocephalus*), twenty individuals out of sixty-seven fall within the range of *leucocephalus*, although not one of these reaches the mean of the latter. Among the grades (7/8 *leucocephalus*), four-fifths of the individuals fall within the range of the latter, while twelve out of fifty-five reach or surpass the mean.

Comparing these animals individually, as before, with their own *leucocephalus* ancestors, we find that not one of the F_2 generation closely approaches its *leucocephalus* grandparent. On the other hand, a single individual falls below (is darker than) its *polionotus* grandparent. Of the sixty-five back-crosses (3/4 *leucocephalus*), one equals and one exceeds the mean value of its *leucocephalus* ancestors. If these two were regarded as pure *leucocephalus* segregants, the proportion would be very close to the expected one where five factor differences are concerned. Of the fifty-five grades, seven (12·7) equal or exceed the mean values of their *leucocephalus* ancestors. On the same assumption as before, we have approximately the expected proportion for seven pairs of factors. Likewise, the distribution of values in this generation (Text-fig. 17) seems inconsistent with any number less than six or seven.

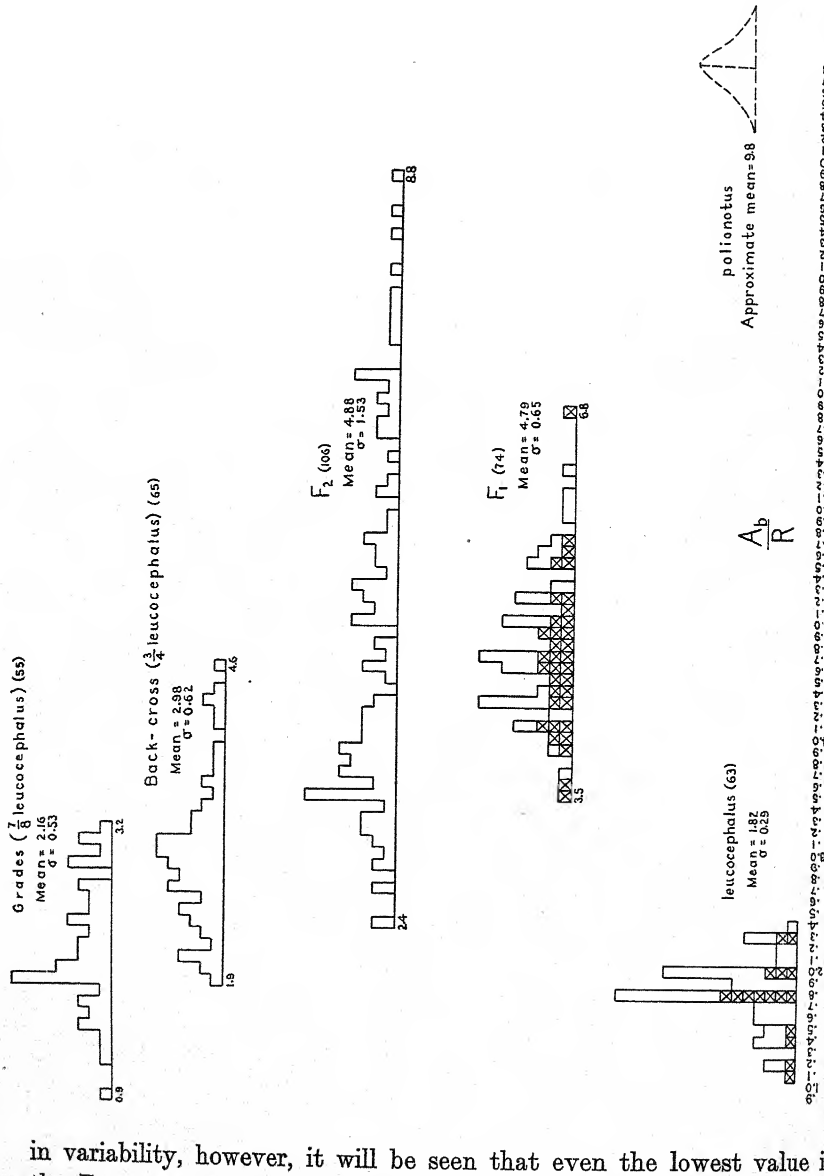
The weighted mean of the parent-offspring correlation coefficients for this character in the present series of animals (excluding that between F_2 and F_3) is $+ 0{\cdot}237$. This is somewhat smaller than the corresponding figure for coloured area. It is likewise smaller than the coefficient for red in the cross previously considered.

The mean of the four coefficients of correlation between the selected F_2 parents and their F_3 offspring is here $+ 0{\cdot}837$. This is also lower than the corresponding figure for coloured area.

$\frac{A_b}{R}$. *Leucocephalus*, as already stated, gives a mean value for this fraction of 1·82. A comparable figure for *polionotus* cannot be given with equal precision for reasons already discussed. An approximate figure would be 9·8. The mean value for F_1 is 4·79, this being somewhat nearer to the value for *leucocephalus* than to that for *polionotus*. The mean for F_2 (4·88) is not significantly different from that for F_1. The corresponding figures for $\frac{A_t}{R}$ are 3·83 (F_1) and 3·82 (F_2). The variability, on the other hand, has increased enormously, the range $\left(\text{for } \frac{A_b}{R}\right)$ having

[1] One F_1 individual falls within the range of *polionotus*.

risen from 3·5 to 6·8 in the F_1, to 2·4 to 8·8 in the F_2. The standard deviations are 0·65 and 1·53 respectively. Despite this great increase



Text-fig. 18. The values here plotted are obtained by dividing the value for coloured area (base) by that for red. They are roughly proportional to the total amount of dark pigment in the pelage.

in variability, however, it will be seen that even the lowest value in the F_2 generation barely falls within the range of *leucocephalus* (Text-fig. 18).

The first and second back-crosses with *leucocephalus* show a progressive shift of the mean toward that of the latter race, while the variability is equal to or less than that of the F_1 generation. In the first back-cross, thirteen individuals fall within the range of *leucocephalus*, although none reach the mean of the latter. In the second back-cross ("grades") thirty-nine, or 71 per cent., fall within the range of *leucocephalus*, while thirteen, or 24 per cent., equal or fall below the mean of the latter. Indeed, one individual gives a lower value than any *leucocephalus*.

Comparing the extreme individuals, as before, with their own pure-race ancestors, we find that not one F_2 individual falls below its *leucocephalus* grandparent, although one gives a higher value than its *polionotus* grandparent. Two back-cross individuals out of sixty-five equal or fall below the mean of their *leucocephalus* ancestors, while among the grades fourteen reach this level. If the individuals in these last two series were counted as pure *leucocephalus* segregants (at least for colour factors), the numbers are in each case such as might be expected for a cross involving five factor differences.

Reference to the histogram for the grades (Text-fig. 18) shows that we have no certain tendency toward a massing of the individuals on the left-hand side of the area. That the asymmetry which is undoubtedly present here has no special significance is probable from the fact that such asymmetry is even more evident in the case of the F_2 and back-cross generations, where it was not to be expected.

$\frac{R-V}{R}$. In respect to this ratio, which represents the richness of colour (or conversely the greyness) of the pelage, *polionotus* does not differ so widely from *leucocephalus*, as does *albifrons*, despite the vastly greater difference in depth of shade, in the former case. The figures for the two former are 35·18 and 27·66 respectively. Furthermore, there is a much broader overlap between the two, some specimens of *polionotus* actually giving lower values than the average *leucocephalus* (Text-fig. 17). It is interesting that the F_1, F_2 and back-cross groups show a mean value for this character considerably higher than the mean of the parental means. This is in keeping with the observed fact that even the palest among these pelages tend toward a richer brown than is commonly met with in *leucocephalus*[1]. In the generation of grades (7/8 *leucocephalus*), however, the mean index of saturation is about the same as in *leucocephalus*.

The usual increase of variability is to be seen here, in passing from

[1] See p. 308.

the F_1 to the F_2 generation. The standard deviation, in this case, rises from 4·49 to 6·05.

Segregants showing aggregate "pure-race" pelage characters. Let us consider, as before, the number of individuals in each of these generations which measure up to the standards of an average *leucocephalus*, in respect to all of the colour characters taken collectively. For this purpose, I have adopted the same procedure as was done for the preceding cross, namely, choosing such limiting values for each of three characters that approximately half of a population of pure *leucocephalus* would be included (see pp. 306–7). As judged by this standard, not a single specimen among the 106 F_2 pelages can fairly be regarded as average *leucocephalus*. In only three cases does the coloured area fall within the prescribed limits. All three of these individuals are excluded, however, both by reason of too low values for red and too high values for the index of saturation. One of them, likewise, has a trace of tail stripe, and two have foot pigmentation of about the average grade for *polionotus*.

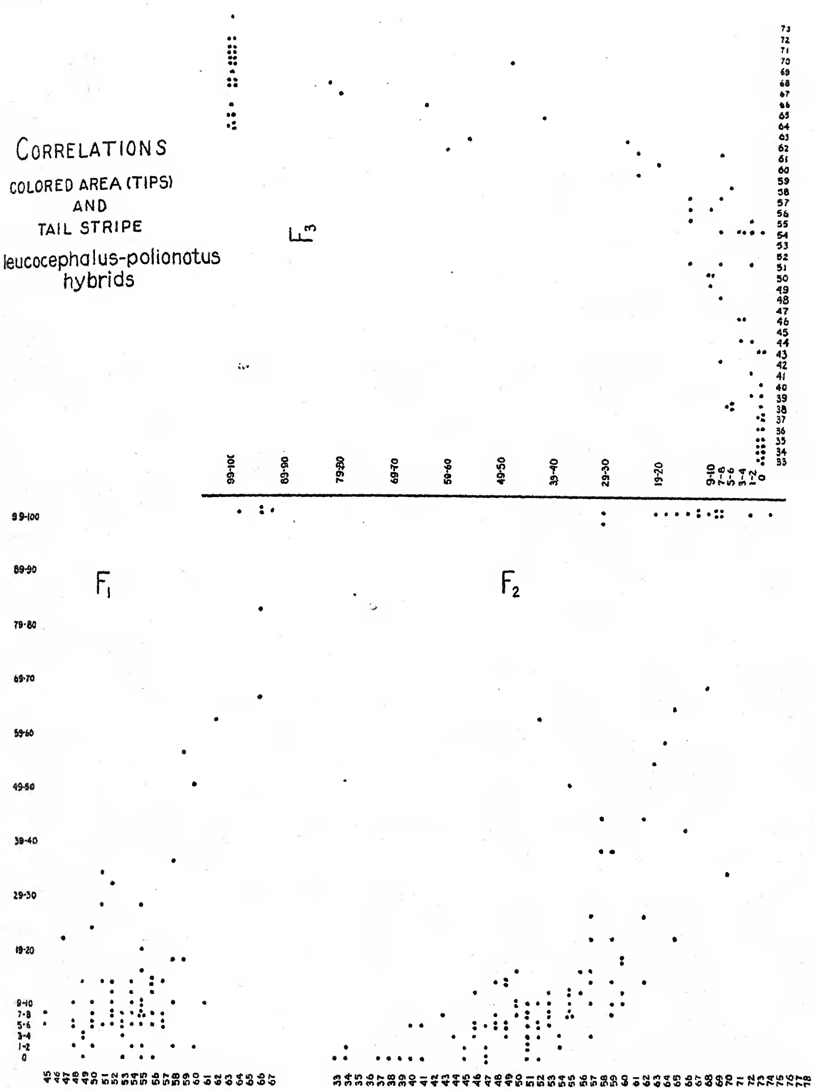
Among the F_3 offspring of selected F_2 parents, thirteen individuals out of eighty-two fall within the prescribed limits in respect to coloured area (A_b). But all of these individuals have too low values for red, and all but one too high values for $\frac{R-V}{R}$, to allow of their inclusion as "average" *leucocephalus*. Half of them likewise show a low grade of foot pigmentation, and two have vestiges of tail stripes.

Among the sixty-five individuals derived from the first back-cross with *leucocephalus*, nine fall within the limits for coloured area, but all of these must be excluded by reason of their values for red or $\frac{R-V}{R}$ or both. In addition to this, the majority display a low grade of foot pigmentation, and one possesses the trace of tail stripe. It may be recalled that, in the *leucocephalus-albifrons* cross, five individuals out of fifty-eight conformed to the requirements for all of the pigmental characters.

It is only when we pass to the grades (7/8 *leucocephalus*) that we meet with specimens which measure up to the standards prescribed for an average *leucocephalus*. Here we have eleven cases out of fifty-five which fall within the limits in respect to all of the pigmented characters. Thirty-two cases would be included, if only the coloured area were concerned, but twenty-one of these fail to conform in respect to one or more of the other characters.

Here, as previously, it is a matter of interest to know whether those individuals which fall within the limits of an "average" *leucocephalus* in respect to colour characters do so likewise in respect to other racial

differences, such as tail and foot length. It has not been regarded as desirable, for these characters, to apply standards of the sort which



Text-fig. 19. Correlations between coloured area (abscissas) and tail stripe (ordinates) in three generations of *leucocephalus-polionotus* hybrids.

were employed for colour characters. However, it may be said that none of these eleven individuals which reach or surpass the "average"

condition (as earlier defined) in respect to colour characters fall appreciably below the mean of *leucocephalus* for tail length, and that seven of the eleven reach or surpass the mean for foot length[1]. All lie well within the limits of variation of the latter race.

Returning to the F_2 generation, we may now enquire whether any of these measure up to the standard set for an average *polionotus*[2]. There are only four individuals which fall within the limits in respect to the value for coloured area. None of these, however, conform to our requirements as regards the other characters. All show too high a value for red, all but one too low a value for the index of saturation, and all but one too low a value for foot pigmentation. In addition, two of the four possess incomplete tail stripes, whereas all of the parent stock of *polionotus* have complete ones.

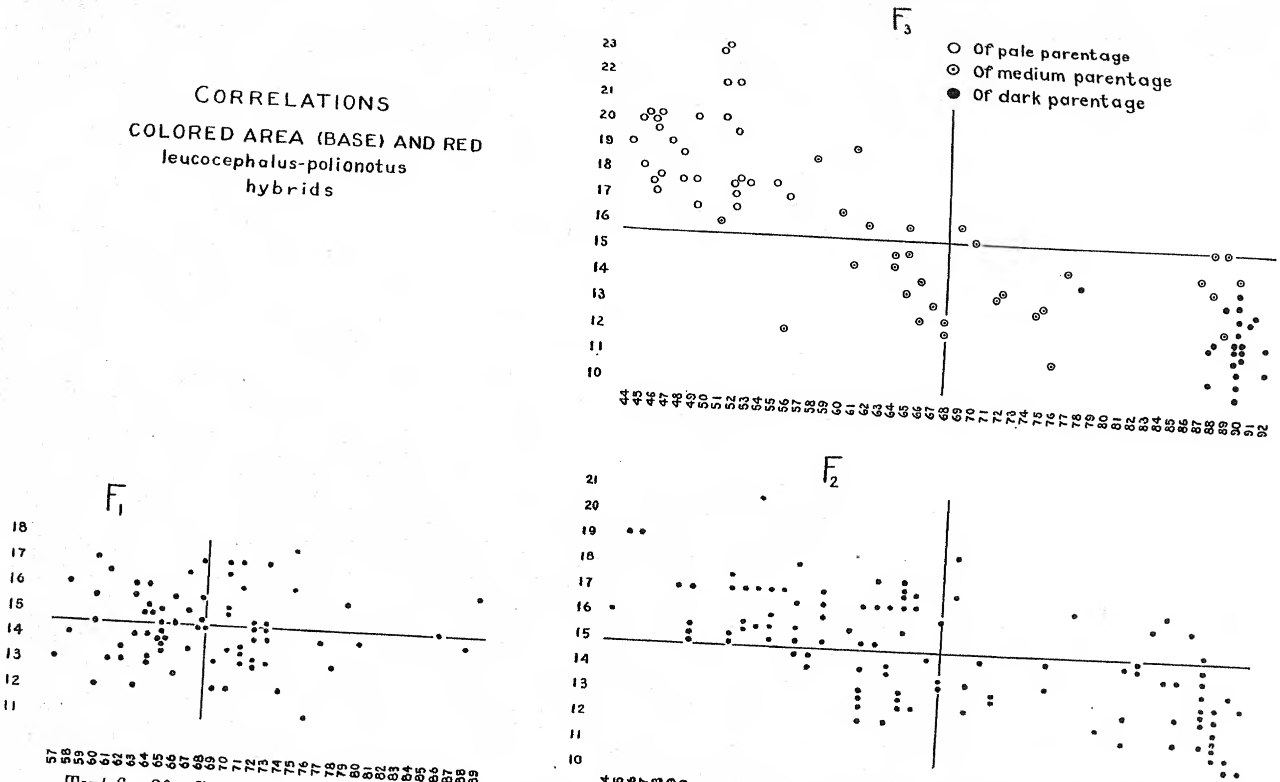
Correlations. The first four paragraphs in the summarised statement under the *leucocephalus-albifrons* series hold, with but slight modifications, for the present one. As regards the second of these we must note a possible exception in the case of foot pigmentation, which is negatively correlated with body length (– 0·205 to – 0·225) in *polionotus* and in three of the hybrid generations for which this has been determined (0, however, in the fourth of these, as well as in the crosses next to be considered).

With respect to the fourth item (Text-figs. 19, 20, 21), the present series furnishes a greater number of illustrative cases than the former series, since certain coefficients were computed here which were not computed for the others. Thus, there appear to be significant correlations (having the "expected" sign) between foot pigmentation and the other pigmental characters. This had been regarded as questionable in my earlier studies of other species (Sumner, 1923, 1925; Sumner and Huestis, 1925).

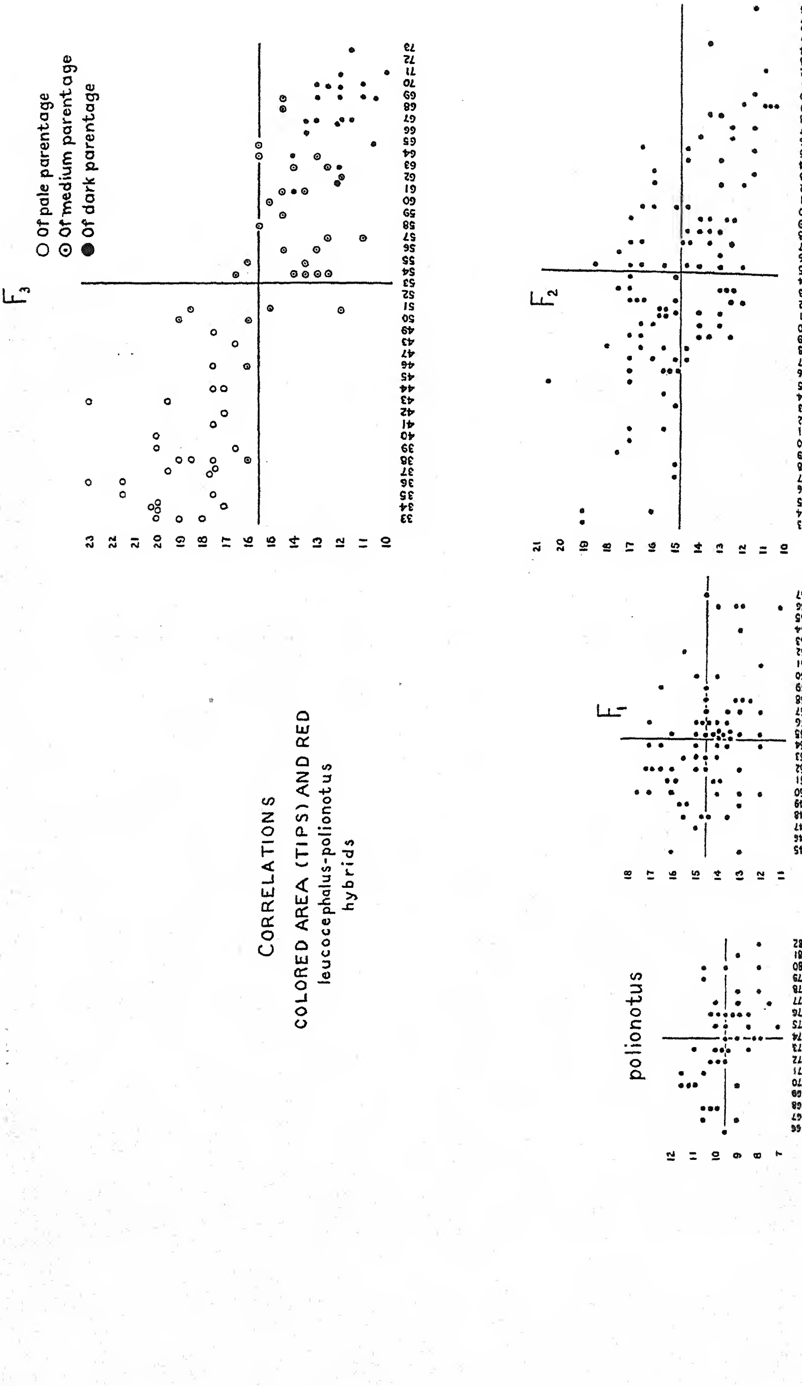
Passing to the fifth of the items previously discussed, we have in the F_3 generation five coefficients of correlation between tail length and pigmental characters, all of which are of the sign which would be expected if there were a tendency for the original racial combinations to reappear. In view of the low value of most of these coefficients, and the fact that

[1] They thus conform, in reality, to a much more exacting standard than was employed for the colour characters.

[2] By setting such limits for each of four characters (A_t, red, $\frac{R-V}{R}$, foot pigmentation) as would include 5/6 of the *polionotus* population, if applied singly, it was found that approximately half (47 per cent.) of the specimens of this race fell within these limits in respect to all four characters. The included values, for each character, were naturally those which tended in the direction away from *leucocephalus*.



Text-fig. 20. Correlations between pelage area pigmented at base (abscissas) and red (ordinates) in three generations of *leucocephalus-polionotus* hybrids.



Text-fig. 21. Same as Text-fig. 20, but for area pigmented to tips.

no such tendency is evident in the larger F_2 series, these might be dismissed as chance results were it not for the similar situation in the cross next to be considered.

As regards foot length, however, the relations are such that it is difficult to attribute them to chance. Of the forty-four coefficients which express the degree of correlation between this character and the various pigmental characters, in the two parent races and five series of hybrids (the sexes being treated separately), the signs of thirty-three are such as to favour the hypothesis of genetic association. Moreover, this preponderance of "expected" signs is due chiefly to the F_2 and F_3 generations, in which we have nineteen out of twenty cases of this sort[1]. A closely similar situation, it will be recalled, was encountered in the *leucocephalus-albifrons* cross.

I have referred to these signs as being the "expected" ones, merely in the sense that they accord with a particular interpretation of the facts. In reality they were quite *unexpected*, on the basis of earlier work. As has been stated previously (Sumner, 1926), I have hitherto found no evidence of a correlation between any pigmental character and the length of any bodily member, although two characters belonging to either of these classes might be strongly correlated with one another.

Owing to the interest which attaches to these correlations between foot length and pigmental characters, if they are real, it is of importance to exclude any possible source of error. Let us enquire, therefore, whether these correlations may not be spurious ones, so far, at least, as any significant biological relationship between these characters is concerned.

The possibility of obtaining by random sampling thirty-one coefficients out of thirty-two[2], having the "expected" sign, would appear to be so remote that any thought of this being a chance result seems absurd. It must be repeated, however, that the evidence is far from being wholly cumulative, owing to the fact that the various pigmental characters here considered are for the most part rather strongly correlated with one another, especially in the F_2 and F_3 generations. It might be suggested that we had here a purely accidental correlation between foot length and *pigmental characters in general*. Accordingly, it has seemed worth while to determine by the method of partial correlation whether, for

[1] Of the parent races, *leucocephalus* shows no tendency of this sort, whereas all of the coefficients computed for *polionotus* are in the "expected" direction. For the hybrid generations (excluding the F_2 and F_3) the results are about equally balanced.

[2] These are the numbers in the F_2 and F_3 generations of both crosses, previously considered. The situation in the *polionotus-albifrons* cross, discussed below, further strengthens this evidence.

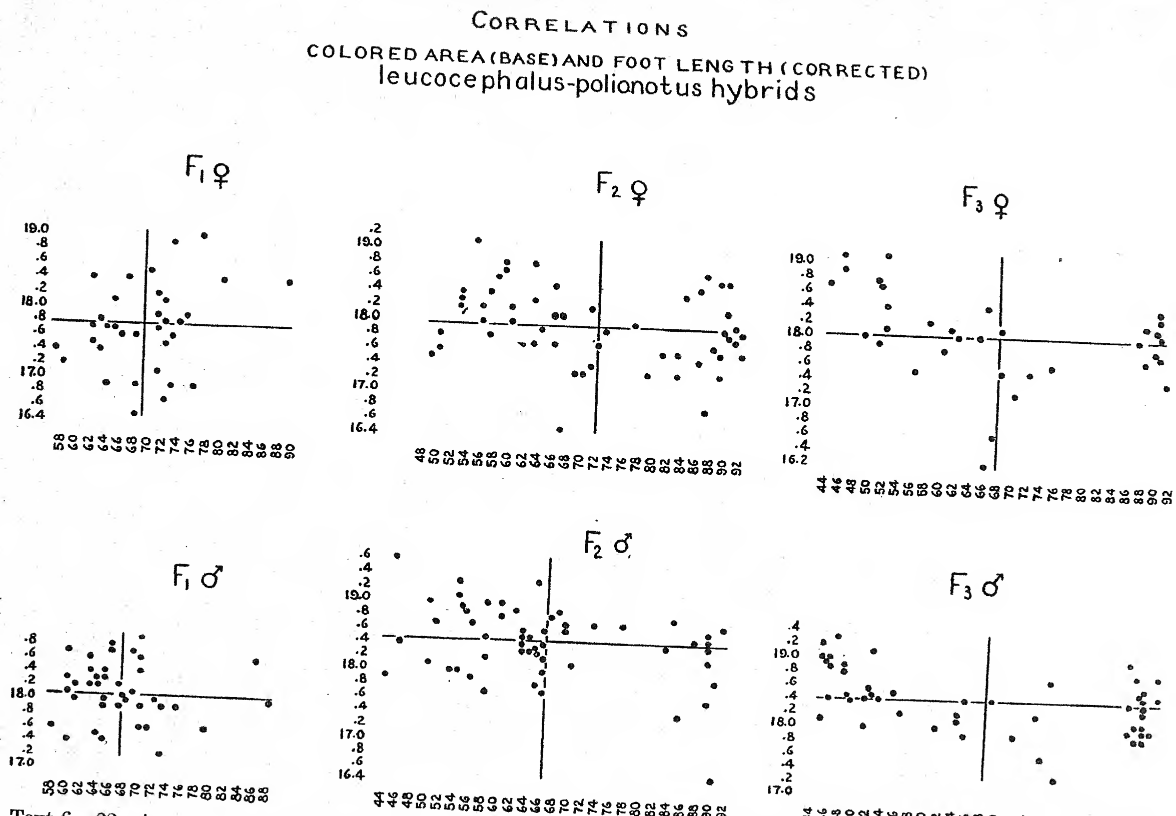
example, any correlation is manifested between foot length and coloured area, independently of the correlation between the former and red, and conversely, whether the correlation with red is to any extent independent of that with coloured area. In the first case (eliminating the influence of red), our four coefficients (F_2 and F_3, male and female) retain the same signs as previously, though in all cases but one they are so reduced in value as to be statistically non-significant when taken singly. In the second case (eliminating the influence of A_t) three of our four coefficients, while greatly reduced, retain the same signs as previously, while the sign of one (previously low) is now reversed.

It thus appears that while much of this correlation between foot length and the various pigmental characters results from a rather close correlation among the latter, there is none the less evidence for an independent correlation between the first-named character and certain of the latter ones, taken separately.

But even if all of the pigmental characters were completely correlated, the probability of such a series of coincidences would be very low, since we are dealing with two generations of two crosses, and in each case the sexes have been treated separately. We should thus have eight independent cases, all giving the "expected" sign, a situation against which the odds would be 255 to 1.

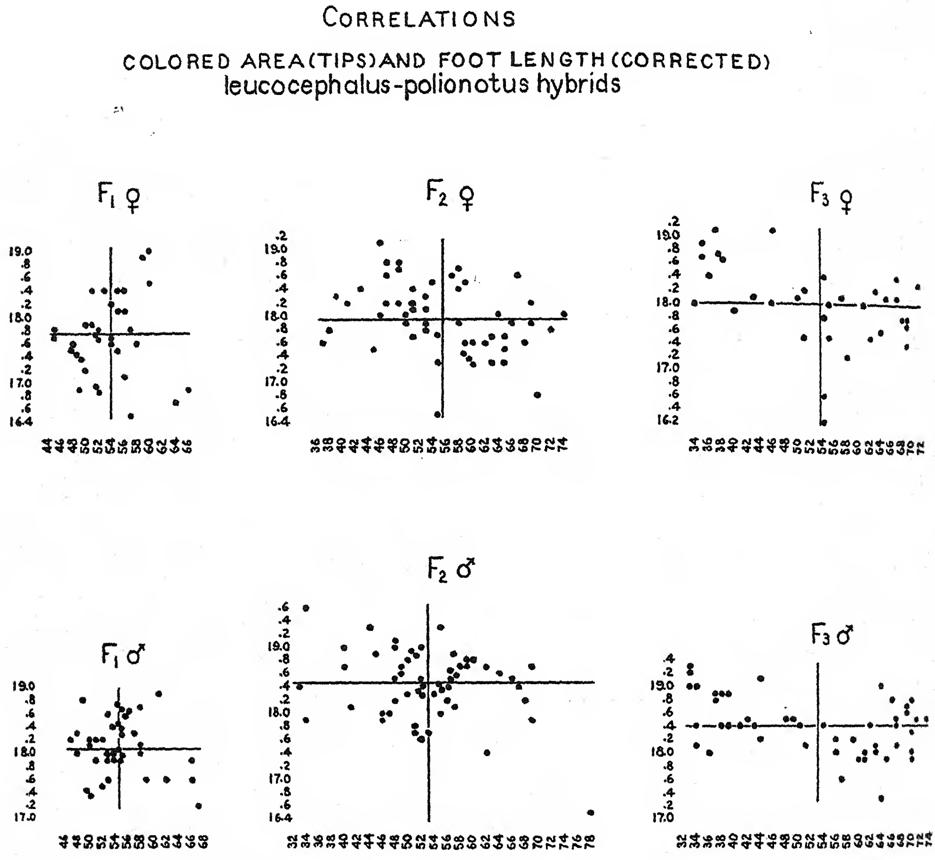
If it be objected that the F_3 generations merely reproduce selected samples of the F_2, and consequently do not furnish evidence independent of the latter, it is sufficient to point out that the parent-offspring correlations between these generations in respect to foot length are low, being 0·114 for the *leucocephalus-albifrons* cross and 0·298 for the *leucocephalus-polionotus* one. Without resorting to the laborious process of computing the partial correlation between foot length and each pigmental character in the F_3 generations (the effects of correlation between these in the F_2 being eliminated), it is clear that no considerable part of the correlation in the former generation can be due to the accidental choice of F_2 parents having this particular combination of characters.

Another circumstance which doubtless favours the existence of correlations between foot length and pigmental characters, in certain cases, is the fact that both may be correlated with general size (body length). In the case of foot length, this correlation with body length is universal, and the coefficients are usually high. With pigmental characters, on the other hand, while coefficients of fair magnitude are sometimes found, the relations are so inconsistent that the influence of size cannot be definitely affirmed except possibly in the case of foot pigmentation.



Text-fig. 22. Apparent negative correlation between pelage area pigmented at base (abscissas) and corrected foot length (ordinates) in the F_2 and F_3 generations of the *leucocephalus-polionotus* cross. (No trace of this in F_1.)

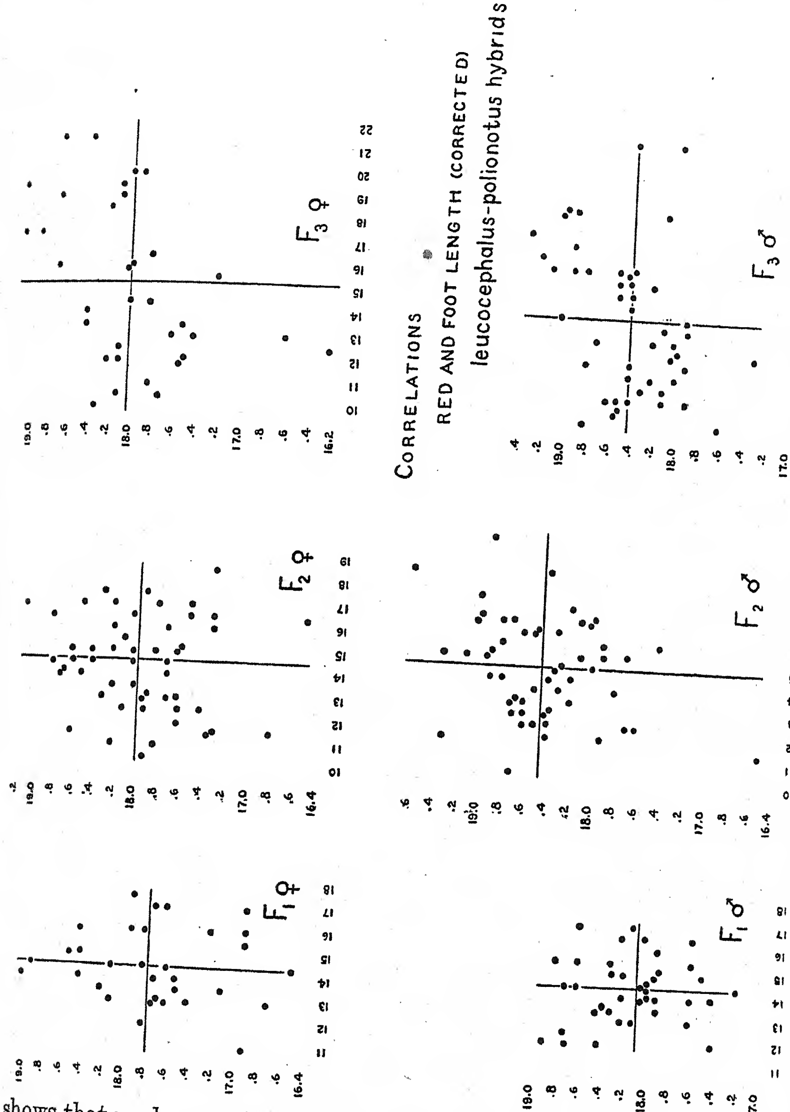
It seems worth while, however, to determine the degree of correlation between foot length and foot pigmentation, after excluding the influence of body length. I shall confine myself to the F_3 generation of the *leucocephalus-polionotus* cross, since the F_2 coefficients are both very low, one indeed furnishing the only instance in either F_2 or F_3 genera-



Text-fig. 23. Apparent correlations as in Text-fig. 22, except that coloured area (tips) has been plotted.

tions of a coefficient with the "wrong" sign. Applying the method of partial correlation, we find that the coefficient for the males is reduced from $-0{\cdot}307 \pm 0{\cdot}09$ to $-0{\cdot}234 \pm 0{\cdot}09$, while that for the females is reduced from $-0{\cdot}390 \pm 0{\cdot}10$ to $-0{\cdot}327 \pm 0{\cdot}10$. Thus these two coefficients, involving the only pigmental character which gives any appearance of being influenced by size, retain a considerable degree of

probability after this influence has been eliminated. In certain other cases, moreover, partial correlation computations would materially *increase* the coefficients. Reference to the graphs (Text-figs. 22, 23, 24)



Text-fig. 24. Apparent correlations between red (abscissas) and foot length (ordinates). In the present case, the correlation is positive, instead of negative, as for coloured area.

shows that we have a distinct, though feeble, appearance of correlation when the foot lengths have been "corrected" for size, *i.e.* reduced to a common body length of 80 mm.

After making allowance, therefore, for all these qualifying circumstances, it still seems probable that we have a correlation, which is not purely accidental, between foot length and the various pigmental characters with which we have dealt, in the F_2 and F_3 generations of both of the crosses thus far considered. The evidence above presented is strongly reinforced by that derived from the *polionotus-albifrons* cross next to be considered.

The sixth paragraph of the summarised statements concerning correlations in the previous cross applies, *mutatis mutandis*, to the present one. The correlations between the various pigmental characters are in nearly all cases of the "expected" sign; that is, we meet with a tendency toward the same association of colour characters within the single populations that is encountered when we compare one geographic race with another (*e.g.* darker individuals, as well as darker races, tend to have more complete tail stripes, etc.). That the correlations between foot length and pigmental characters, in the F_2 and F_3 generations, correspond to the manner in which these characters are combined in the parent races has already been pointed out. Such an apparent genetic association is perhaps surprising in the crosses involving *albifrons*, since in this sub-species foot length may undergo marked local variation, to a large degree independently of pelage colour (see footnote on p. 281).

The statements regarding the relative magnitude of the correlation coefficients in the F_1, F_2 and F_3 generations (paragraph 7) likewise hold with even greater force for the present cross[1]. Except for cases involving the index of saturation, the correlations among the pigmental characters for these three generations form a series of increasing magnitude. The most striking instance of this, in the present case, relates to the correlation between the two measurements of coloured area (A_b and A_t). These rise from + 0·458 in the F_1 to + 0·891 in the F_2 and + 0·951 in the F_3. As has already been stated, consistent correlations between foot length and pigmental characters are met with only in the F_2 and F_3 generations. In the present cross, these coefficients are with a single exception higher in the F_3 generation than in the F_2.

Finally, the facts regarding correlation between the index of saturation and other pigmental characters may be expressed in much the same language as for the preceding cross. The meaning of some of the differences in the value of the coefficients is not clear, but the fall of the correlation with red from + 0·700 in the F_1 to + 0·364 in the

[1] Huestis (1925, p. 464) reports several instances of increased correlation between hair characters in the F_2 generation.

back-crosses with *leucocephalus*, and to − 0·177 in the grades (7/8 *leucocephalus*), is in accordance with expectation, and agrees with the trend shown in the *leucocephalus-albifrons* cross (p. 314).

(*c*) *The* polionotus-albifrons *series.*

(Text-figs. 25–27.)

The results from this series are less satisfactory in a number of ways than those from the two previously discussed. (1) Only two hybrid generations were reared, there being an F_1 generation, and back-crosses with each of the parent races. (2) *Albifrons* of both the East Pass and the Foster's Bank collections, and ones of mixed descent, were used indiscriminately, and it has not been practicable to separate the derivatives of the two sub-races, as has been done in the case of the *leucocephalus-albifrons* cross[1]. There are, nevertheless, various points of considerable interest to be noted in connection with this series of hybrids.

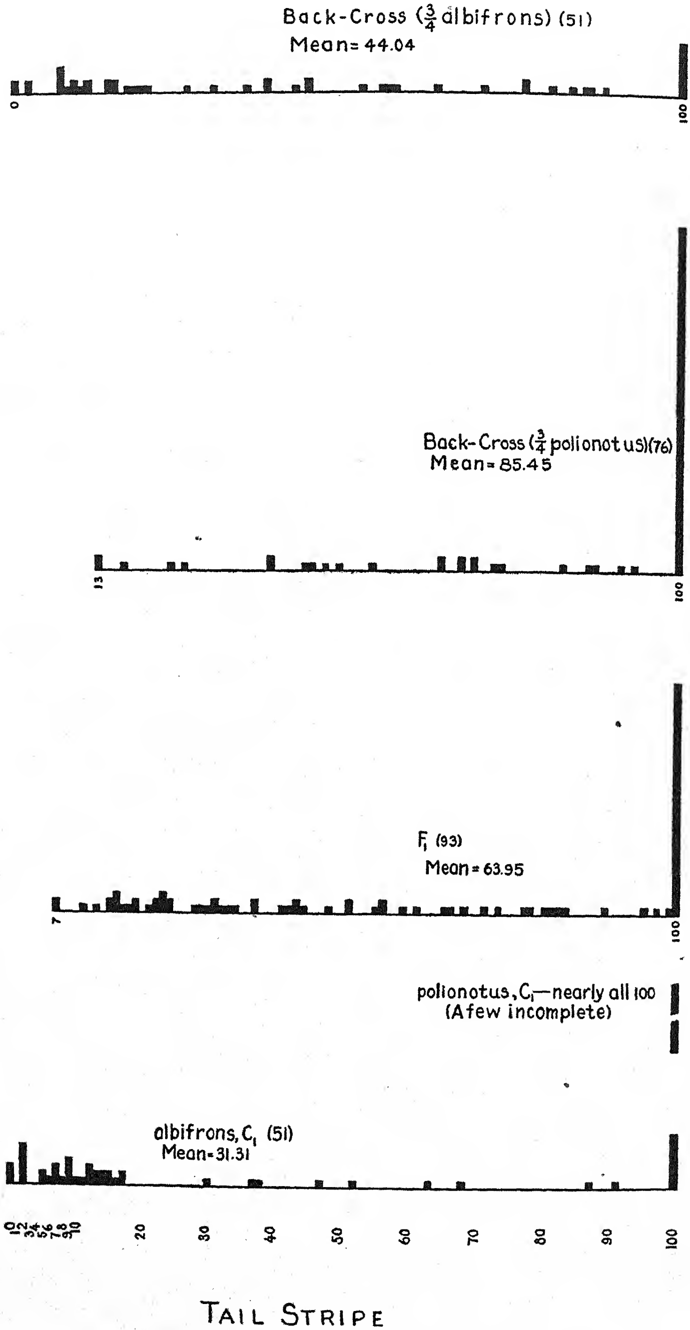
It is not worth while to consider the behaviour of all of the various characters in turn, as has been done for the two preceding crosses. I shall accordingly pass over the linear measurements of bodily parts and proceed directly to the discussion of pigmental characters.

The mean value of the tail stripe in the F_1 generation (63·95) is about midway between those of the parent races (100 and 31·31)[2]. This is in striking contrast with the results of crossing either of these races with *leucocephalus*. It will be recalled that the stripeless condition of the latter sub-species is dominant, though incompletely so, over the condition found in either *albifrons* or *polionotus*. Back-crosses with the two parent races give mean values of 44·04 (*albifrons*) and 85·45 (*polionotus*) respectively. It will be seen from the graphs that there is an enormous range of variability within each series (Text-fig. 25).

The behaviour of *foot pigmentation* is less intelligible. Whereas the mean values in the wild *polionotus* and *albifrons* respectively are 1·47 and 0·07 (1·97 and 0·25 in the C_1 generations), we have a value of 1·44 in the F_1 generation, and 1·75 and 0·98 respectively in the back-crosses with *polionotus* and *albifrons*. Attention has already been called to the deeper foot pigmentation of cage-bred series of these mice (p. 321). This fact, together with a partial dominance of the deeper pigmentation, would explain the results fairly well.

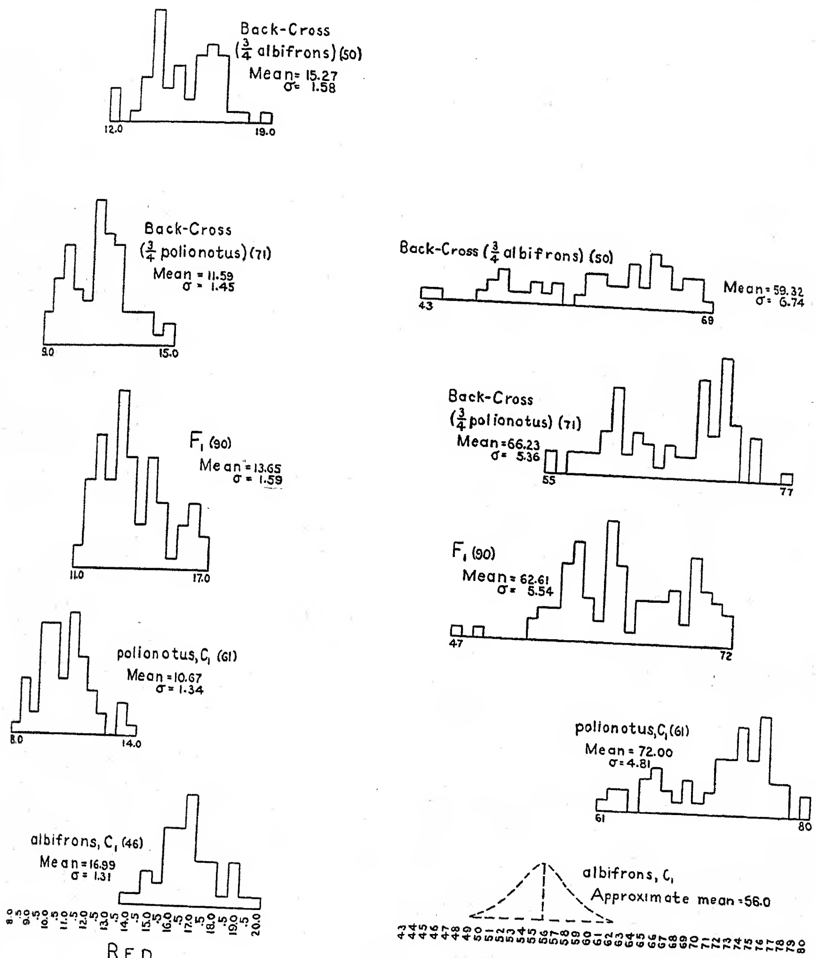
[1] Likewise, no skeletons have been prepared of the *polionotus-albifrons* series.

[2] C_1 (cage-bred) animals were here used as parents both of the F_1 and the back-cross generations. But the data for many of the C_1 series of *albifrons* are unfortunately incomplete, to such an extent that the mean values for actual parents cannot be profitably computed.



Text-fig. 25. Tail stripe in the *polionotus-albifrons* cross.

As regards the value for *red*, the F_1 generation is likewise about midway between the parent races. A fair comparison cannot be made in the case of *coloured area*, since figures for the C_1 lot of *albifrons*, which



Text-fig. 26. Red and coloured area (here the area occupied by hairs pigmented to their tips) in the *polionotus-albifrons* cross.

were the ones used in the present cross, are available only for A_b, while measurements of A_t alone were made for these hybrids (Text-fig. 26).

It may be recalled that *polionotus* and *albifrons* (at least the coast representatives of the latter) present one absolute point of difference,

the presence and absence of basal pigmentation in the ventral hair[1]. Such being the case, interesting relations might have been expected with regard to this character. But nothing very instructive is to be observed. In the F_1 generation it is probable that all individuals display at least a trace of such pigmentation, while most of them display much more than this. In the back-cross with *polionotus* the hairs of the ventral region, in practically all specimens, are plainly pigmented at the base. An enumeration of the 3/4 *albifrons* specimens, on the other hand, shows that twenty-five belong to the 0 grade, while the remaining twenty-six display conditions ranging from "trace" to "pronounced." Here we might be disposed to find an excellent case of a 50 : 50 ratio. But the significance of such an interpretation is largely nullified by the existence of a very strong fraternal correlation for this character. Thus, within the single fraternities, there is very little evidence of "splitting."

In the present cross, no general increase in variability is evident in the back-cross series, as compared with the F_1. This is curious, in view of the evidence for segregation in the back-cross generation which will be offered shortly.

Of the sixty-seven individuals resulting from the back-cross with *polionotus*, eight have values for coloured area which equal or exceed those of the means of their own *polionotus* ancestors. This would be almost one in eight. However, the significance of this fact is rendered uncertain by the circumstance that four out of eighty-two individuals in the F_1 generation have values which equal or exceed those of their *polionotus* ancestors. I have not looked up individual pedigrees for the values of red.

The back-cross with *albifrons* will not be considered here, owing to the fact that comparable measurements are not available (see above)[2].

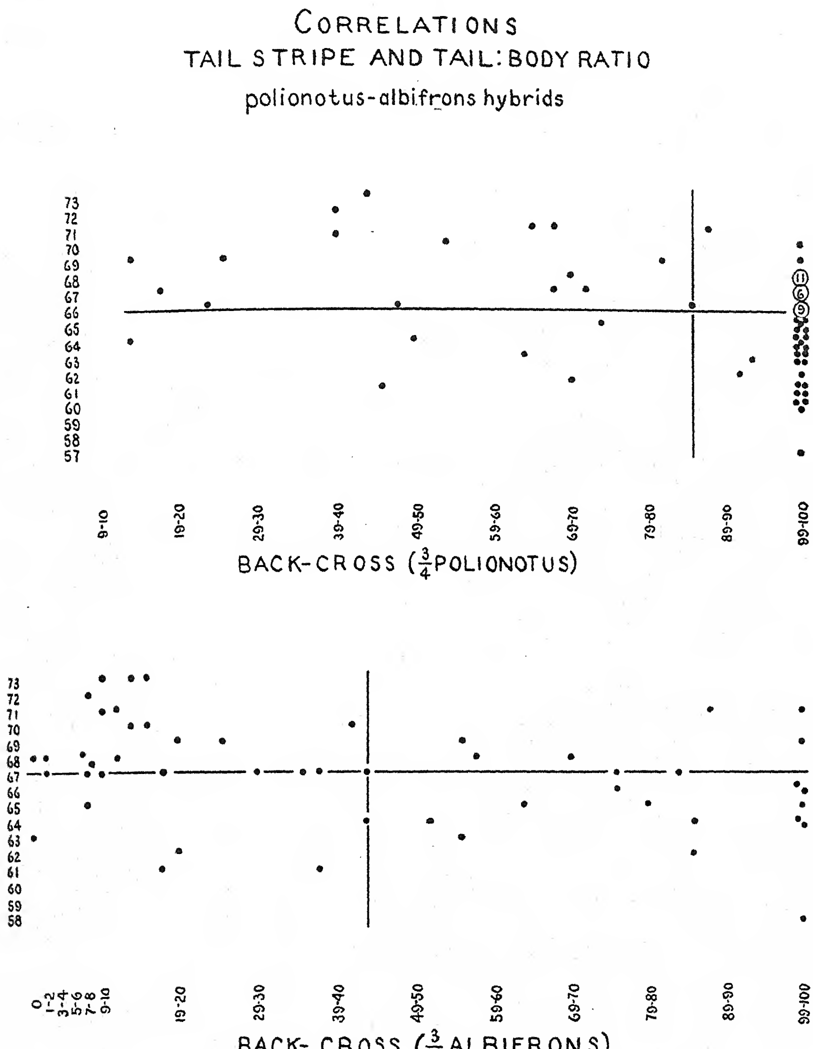
Parent-offspring correlations between certain generations have been determined, but only for foot pigmentation and coloured area. In conformity with my earlier procedure, I have computed the weighted mean of the correlations between "wild" and C_1 generations of the parent races, between the parent races and the F_1 generation, and between the latter and the back-cross generations. The first-named character gives a mean value of + 0·116, the second + 0·422.

All of those correlations between various characters which were found to be indubitably present in the two preceding crosses are manifested in

[1] Sumner (1929).

[2] It likewise happens that half of the *albifrons* ancestors of this series died prematurely, so that measurements of these characters were not obtained.

the present series. In both of the back-cross series, aggregating 127 individuals, there is a consistent correlation between the length of tail and foot



Text-fig. 27. Apparent correlations between tail stripe (abscissas) and relative tail length (ordinates) in *polionotus-albifrons* cross. Where the number at a given locus is too great to be represented by individual dots, this is indicated by the figure in the circle.

and the various pigmented characters. Coefficients were computed for the correlation between the length of each of these members and the four pigmental characters—tail stripe, foot pigmentation, coloured area (A_t)

and red. For the correlations involving foot length the sexes were dealt with separately. There are thus twenty-four coefficients. It will be noted that in every case but one (this being non-significant), these coefficients are of the sign which would be expected on the assumption that racial differences in these two classes of characters tend to segregate together. Thus tail and foot length are negatively correlated with tail stripe, foot pigmentation and coloured area, but are positively correlated with red. The latter value, it will be recalled, is a measure of the degree of pallor, *i.e.* of the *absence* of dark pigment.

It is curious that this preponderance of "expected" signs occurs among the back-crosses, in the *polionotus-albifrons* series of hybrids, whereas, in the two preceding series, it was displayed only by the F_2 and F_3 generations, not being evident in the back-crosses. Also, it is as evident here in the case of tail length as in that of foot length, which was not true of the previous crosses (see Text-fig. 27).

One qualifying circumstance must here be mentioned. Examination of individual pedigrees reveals the fact that a certain proportion of this correlation is due to the employment of two different strains of *albifrons*, as parents of these back-cross generations. Thus, as stated earlier, the East Pass strain possesses shorter feet and more extensive coloured area and tail stripe than the Foster's Bank strain, and these differences persist in their descendants, whether pure or hybrid. But it is likewise clear that this circumstance is responsible for only part of the correlations here considered, and that it has no effect, or even a reverse one, in some of the cases. The statistical force of this array of coefficients is thus somewhat weakened, but it is by no means destroyed[1].

Aside from the facts just considered, it must be repeated that these twenty-three coefficients do not have an altogether cumulative value, since tail and foot length are correlated with one another, on the one hand, and all of the pigmental characters are correlated on the other.

(*d*) *An interspecific cross.*

As stated above, one F_1 female was derived from a cross between *P. maniculatus sonoriensis* and *P. polionotus leucocephalus*. This female was successfully mated with a male *leucocephalus* and with a male *P. maniculatus gambelii*. The former back-cross yielded two offspring, the latter thirteen.

[1] The circumstance here referred to does not, of course, affect either of the crosses previously considered. Only the East Pass derivatives have been considered in dealing with the *leucocephalus-albifrons* cross.

Certain facts relating to these hybrids are of considerable interest, despite the small numbers of animals concerned. The single F_1 female plainly displays characteristics derived from both of the species which entered the cross. In body length, it is at least equal to an average adult female *sonoriensis*, *i.e.* to the larger race[1]. In tail and foot length, on the other hand, it is intermediate, but in the former character it stands much nearer the average for the shorter-tailed *leucocephalus*. Tail stripe is almost completely lacking, having a value of about 3 per cent. of the exposed part of the tail. Here, as in the crosses previously considered, lack of tail stripe is dominant, though imperfectly, over its presence. It is always complete in normal specimens of *sonoriensis*. The coloured area is paler than in any except the palest *sonoriensis*[2], and its extent is greatly reduced, in comparison with the latter race, both on the head and the body. The influence of *leucocephalus* is further manifested in the presence of an extensive ventral area having hair which is white throughout its entire length. This condition is not present in any member of the *maniculatus* series, so far as I am aware. As in the case of *leucocephalus*, *albifrons* and the majority of hybrids considered in the foregoing pages, there is a region of hairs which are pigmented only at their basal zone, lying between the externally visible coloured area and the area of pure white hairs.

Passing to the thirteen offspring resulting from back-crossing with *maniculatus*, the coat colour of the majority would be matched very closely in a collection of *sonoriensis* skins, though the shade of the darker individuals lies closer to *gambelii*[3]. The ventrolateral whitish areas of most of them are, however, paler and more extended than in any specimens of the latter race. But, in every case, this area consists of hairs which are pigmented fairly heavily at the base. The most interesting feature of these back-cross animals relates, however, to the tail stripe. Of these thirteen individuals, six have a complete and normal tail stripe, though in one case this is not very intense, as not infrequently happens even in pure *maniculatus*[4]. Seven individuals, on the other hand, have very incomplete tail stripes. Five of these terminate short of the middle

[1] The *maniculatus* group, as a whole, comprises mice of much larger size than the *polionotus* group.

[2] It may be closely matched in shade by many *albifrons*.

[3] *Gambelii* and *sonoriensis* overlap rather broadly in respect to general shade. Data are not at present available for satisfactory quantitative comparisons between the latter races and these hybrids.

[4] No measurements of the width of the stripe were taken. It appears, to the eye, to be slightly narrower than in *gambelii*.

of the tail, while in all cases the stripe is very faint, and consists of scattered black hairs. To the eye the tail stripes here comprised thus fall into two quite distinct classes, and the ratio is as near the traditional 50 : 50 as is possible with these numbers. If this case stood alone, we might easily recognise here a rather clear case of the segregation of a character difference dependent upon a single pair of Mendelian factors. But the lack of any such simple segregation in crosses between the much more closely related races previously considered renders this interpretation highly questionable.

The two specimens derived from the back-cross with *leucocephalus*, as might be expected, resemble the latter race much more closely. They were skinned when less than 3 months old, so that the pelage is not fully mature. That of one may be matched fairly well by some of the darkest specimens of *leucocephalus*; in the other, the coloured area is much too extended to allow of such comparison. It is of possible significance that the member of this brood (both are males) which resembles *leucocephalus* closely is also much smaller than the one which is less like the latter. Likewise, the length of both tail and foot in this smaller specimen is considerably less, both relatively and absolutely, thus approaching rather closely, in these respects, the means for *leucocephalus*. It is unfortunate that circumstances prevented the rearing of further hybrids between these species.

V. Summary and general discussion.

It is possible that the reader who has examined the foregoing data may have been more impressed by the inconsistency and inconclusiveness of some parts of the evidence than with the decisiveness of other parts. The criticism may be brought with some justice that we are dealing throughout with too many variables. It would of course have been far preferable, had this been possible, to maintain the same environmental conditions, including food, as are normal for these animals in a state of nature. Likewise, for the purposes of the hybridisation experiments, at least, it would have been far preferable to deal with genetically homogeneous stocks. However, these things were not practicable, though I realise their desirability as much as any critic. Let us, then, make the most of what we have.

Before proceeding to discuss some of the broader problems here involved, I shall introduce an itemised summary of the results presented in the foregoing pages.

(1) The geographic races of mice, chiefly here considered, differ from

one another rather strikingly in the quantity and distribution of pigments in the hair and skin, and also differ, though less strikingly, in certain details of bodily proportions. In total size, these races are approximately equal. In the case of the single interspecific cross, the two species differ considerably in general size, as well as displaying, in an even higher degree, all of the other classes of differences just mentioned.

(2) The pigmental characters of the geographic races bear definite relations to certain environmental gradients. The linear measurements of body parts, while exhibiting local differences, show no such constant relations.

(3) The mean racial differences in both linear and colorimetric characters are entirely genetic. Stocks of different races fail to converge when reared for a number of generations in a common environment.

(4) Individual differences within a single race are partly genetic, as appears from coefficients of correlation between parents and offspring, or between other groups of related individuals. These individual differences relate to the same bodily "characters" as do the racial differences.

(5) Individual differences are, however, to a considerable extent non-genetic, as is shown by the relatively low values of most of these parent-offspring correlations, and by the observed fact that some characters, particularly the length of certain members, are demonstrably affected by environmental conditions.

(6) As regards the degree of distinctness which is shown by two races subjected to hybridisation, the characters herein dealt with fall under three heads: (*a*) characters which are invariably present in full measure in one race and invariably absent in another (*e.g.* tail stripe and pigmentation at base of ventral hair in the *leucocephalus-polionotus* cross; pigmentation of ventral hair in the *polionotus-albifrons* cross); (*b*) characters which are present in both races, but which vary so widely in degree that there is no overlapping of the distribution "polygons" for the various values (*e.g.* red and coloured area in all three of the racial crosses); (*c*) characters in which the two races differ in respect to the mean values shown, but in which there is a more or less broad overlap of the individual values (*e.g.* the index of saturation, tail and foot length and bone measurements, in all three crosses).

(7) In respect to all of these racial differences, both linear and colorimetric, the first as well as the later hybrid generations show an intermediate condition. For most characters, the mean value in the F_1 and F_2 generations is approximately midway between the parental means, *i.e.* there is no appreciable dominance.

(8) Dominance is strikingly shown, however, in the case of one character, tail stripe. Lack of tail stripe is dominant, though incompletely so, over its presence, this phenomenon being clearly illustrated in two inter-racial crosses, and in one inter-specific cross. This dominance is of the "fluctuating" type, there being an enormous range of variability in the first hybrid generation (at least in the sub-specific crosses).

(9) Dominance is less strikingly shown in the case of another pigmental character, relative pallor or darkness of the pelage, represented by the value for "red" (R) in the preceding pages. A dark pelage (indicated by a low value for R) is incompletely dominant over a paler one. There also appears to be a tendency toward dominance of a richer coloration of the pelage over a greyer one, as indicated by values of the fraction $\frac{R-V}{R}$.

(10) The facts cited in the two preceding paragraphs are rather unexpected, inasmuch as the degree of development of the tail stripe is negatively correlated with "red" (*i.e. positively* correlated with depth of pigmentation). Yet presence of tail stripe is recessive, while depth of pigmentation tends to be dominant.

(11) In the case of the first two of these characters which display a partial dominance, there is a shifting of the mean in the recessive direction in the F_2 generation, as compared with the F_1.

(12) In no case does our evidence indicate that a racial difference in respect to any distinguishable character is dependent upon a single pair of Mendelian allelomorphs. This is evident from an inspection of the graphs. In the one instance in which we have the appearance of a secondary mode in the F_2 generation (Text-fig. 14) it was shown that a one-factor interpretation was quite improbable. Likewise, the seeming presence of a single factor having visible effects upon the tail stripe, in the inter-specific cross (p. 350), is very doubtfully open to such an interpretation.

(13) That genetic segregation occurs, none the less, in respect to one important class of characters at least, is conspicuously shown by the graphs for the various measurements of the intensity and extensity of pigmentation, as well as by the relative magnitudes of the standard deviations for the F_1 and F_2 hybrid generations, as shown in the tables. It is most conspicuous in the widest of these crosses (*leucocephalus-polionotus*), though quite pronounced in the *leucocephalus-albifrons* cross. The two back-cross generations show rather erratic relations in this respect.

(14) As regards the linear measurements of body parts, there is, on

the contrary, little or no evidence of segregation. The standard deviations of the F_1 and F_2 generations have been compared for seven sets of linear measurements (tail, foot, ear, certain bones), considered separately for the two sexes. In the *leucocephalus-albifrons* cross the F_2 figure is actually more often smaller than larger. This is true both for the "actual" and the "corrected" values. In the *leucocephalus-polionotus* cross, on the other hand, in which the differences between the parent races are much more pronounced, the F_2 figure ("actual") is larger than the F_1 in eleven cases out of fourteen, though this proportion falls to nine out of twelve, when "corrected" values are considered[1]. In both of these crosses the standard deviations for number of caudal vertebrae are greater in the F_2 than in the F_1 generation. It must be said, however, that the differences, taken singly, are in most of these cases trivial.

(15) The number of genetic factors commonly concerned in any single character difference is probably considerable. Various estimates of these numbers are obtained by various methods of calculation. It is likely that the lowest of these are erroneous.

(16) In the narrower *leucocephalus-albifrons* cross several individuals in an F_2 generation of seventy-four reach or surpass the mean of one or the other parent race in respect to the value of coloured area or of red. Even in the wider *leucocephalus-polionotus* cross two or three individuals out of 106 reach the mean of each parent race in respect to the value of coloured area, though not of red. One individual, however, reaches the value of red of its own *polionotus* grandparent.

(17) If we provisionally consider those individuals which reach or surpass the mean of one parent race, with respect to a given character, as "pure" segregants for that character, and base our computations upon the F_2, and the first and second back-cross generations of the *leucocephalus-albifrons* and *leucocephalus-polionotus* crosses, respectively, we reach the following estimates. The difference between *leucocephalus* and *albifrons*, in respect to the magnitude of the coloured area, is determined by about four factors (two to six), the difference in their values for red being determined by two to three factors. On the other hand, the relative magnitudes of coloured area in *leucocephalus* and *polionotus* would seem to depend, according to this method of computation, upon between three and four factor differences, while the relative magnitudes of red would depend upon three to five factor differences. Similar estimates are obtained if we rank as a "pure" segregant any individual

[1] The latter are not given for skull breadth, hence the difference in total number.

which reaches or surpasses its own particular ancestor (or ancestors) of one or another race, in respect to a given character.

(18) That most of the estimates above given, aside from their manifest inconsistencies, are too small would seem to be indicated by a comparison of the histograms for the "grades" (7/8 *leucocephalus*) with the theoretical distribution of values in a generation of this composition (Text-fig. 15).

(19) In the *leucocephalus-albifrons* cross 15 and 18 per cent. respectively of the F_2 individuals fall within the extreme range of one or the other parent race in regard to all of the pigmental characters here considered, taken collectively. About two-thirds as great a proportion, however, fall within these limits, even in the F_1 generation. In the wider *leucocephalus-poliònotus* cross, on the other hand, not a single individual in either of these generations falls within the limits of *leucocephalus* for all of the pigmental characters, although three F_2 individuals fall within the limits of *polionotus*.

(20) If we seek for individuals which measure up to the "average" condition of one or another of our pure races in respect to the ensemble of pigmental characters (*i.e.* a standard which would include half of the population of a given pure race) we do not find a single such case in the F_2 generation of either of our two principal crosses. A number are excluded from one or the other class in the *leucocephalus-albifrons* cross, only because they fail to conform to the standard set for the index of saturation. Thus, the richness of coloration has been found to be inherited to a considerable degree independently of either the depth or the extensity of pigmentation. Five out of fifty-eight back-cross individuals, and nine out of forty-one, among the grades, in the *leucocephalus-albifrons* cross, conform, however, to the standards set for an "average" *leucocephalus*. In the *leucocephalus-polionotus* cross we do not meet with any cases of this sort until we reach the grades, among which we find eleven out of fifty-five which may be rated as "average" *leucocephalus*.

(21) In both pure races and hybrids the length of certain members (tail, foot, ear) is found to be positively correlated, even when the influence of general body size has been eliminated by the method of partial correlation. Longer tailed individuals, like longer tailed races, tend to have longer feet[1]. There are, however, no significant differences between the hybrid generations in respect to the magnitude of these correlations.

[1] Such inter-racial correlations do not hold, to be sure, for ear length.

(22) The various pigmental characters are likewise correlated with one another, both in the pure races and the hybrids, and here again intra-racial correlations are of the same sign as inter-racial ones (*e.g.* coloured area and red are negatively correlated, within each population, just as the race having the most extended coloured area has the lowest value for red, and *vice-versa*).

(23) The last named correlations are commonly lowest for the pure races and F_1 hybrids (lowest of all, frequently, in the latter); higher for the F_2 generation, and highest of all in the F_3 generation, derived from selected F_2 parents. The coefficients for the back-crosses are variable, though much more often higher than lower, in comparison with those for the F_1.

(24) These relations are, for the most part, such as might be expected, on the supposition that the characters concerned are in some way genetically connected, and that they therefore tend to segregate together. Reasons will be advanced below for believing that these correlations are due to the diverse effects of the same genetic factors, rather than to separate factors bound together by linkage.

(25) This common genetic basis for all the various pigmental characters is not, however, absolute. There is a considerable degree of independent variability among these characters, and it may be shown that a large fraction of this independent variability is genetic. Thus, two pigmental characters may be supposed to have certain factors in common and certain ones peculiar to themselves.

(26) There is some evidence for the existence of correlations between the bodily appendages (tail and foot) and the pigmental characters, in certain of the segregating generations of hybrids, in all three crosses. The coefficients are preponderantly of the "expected" sign, on the assumption that the character differences of a sub-species should segregate together. While the considerable series of coincidences here displayed can hardly be credited to random sampling, there are circumstances which render the foregoing interpretation somewhat questionable.

In the ensuing discussion I shall consider in succession three chief topics: (1) the possibility of determining the approximate number of genetic factors concerned in these racial differences; (2) the significance of the correlations which exist between certain characters, particularly in the segregating generations of hybrids; (3) the bearing of the present data upon our conceptions of evolution.

To those who accept the view that one species or race differs from

another by a definite number of mutational steps, it is, of course, a matter of considerable interest to determine, if possible, the approximate number of such steps which separate one given form from another. It was, at the outset, my hope that some of the "presence-or-absence" differences, belonging to the first (*a*) class of characters listed in paragraph 6 of our summary, would lend themselves to a Mendelian analysis of the characters concerned. But this did not prove to be the case. For in the F_1 generation such characters were found to have an intermediate value, and to be extraordinarily varied in their manifestation. Thus, the length of the tail stripe of the F_1 generation (heterozygous for all factors concerned) covered the whole gamut from 0 to 100 per cent. Back-crossing with the 0 grade race (*leucocephalus*) led to a great increase in the proportion of stripeless individuals, and the disappearance of all except the lower grades of tail stripe. But since it is probable that the 0 grade consisted, in this generation, largely of individuals which were heterozygous for some or all of the factors concerned, it is plain that the proportionate number of individuals which lack the stripe altogether, as contrasted with those which possess it at all, affords no clue to the genetic classes which may be present. Furthermore, it seems certain that, with each back-cross to *leucocephalus*, an increasing proportion of the partially heterozygous individuals must fall within the 0 grade, and conversely that the relative number which show some trace of a stripe must decrease. It would thus seem to be futile to conduct such a "dilution" process in the hope of arriving at any single-factor difference in a case of this character.

Accordingly, we seem limited, in our quest for the number of factor differences between any two races, to characters which differ merely in degree (*b* and *c* of the classes listed above). Now it has already been abundantly shown that the evidence in such cases is conflicting. This has not infrequently been the experience of others.

It will be recalled that Castle and Wright (Castle, 1921) developed a formula for determining the number of factor differences concerned in a cross involving quantitative characters. Their formula was:

$$n = \frac{D^2}{8\,(\sigma_2{}^2 - \sigma_1{}^2)},$$

in which D is the difference between the parental means, in respect to the given character, and σ_1 and σ_2 are the standard deviations in the F_1 and F_2 generations, respectively. This formula was severely criticised by Shull (1921), and has recently been dealt with more fully by Serebrovsky (1928). The chief grounds for criticism are three: (1) that a

complete lack of dominance is assumed; (2) that the factors are assumed to be of equal potency; and (3) that all of the positively working factors are assumed to be on one side of the cross, and all the negatively working ones on the other. Serebrovsky works out supplementary formulae, covering varying degrees of dominance, and differing distributions of positively and negatively working factors in the two races. Philiptschenko (1929), however, finds himself led to impossible results, even with the use of Serebrovsky's modified procedure. Castle (1928) admits that he has not found the results from the use of his own formula satisfactory, and queries whether the trouble may not lie with the fundamental postulates of the multiple factor hypothesis itself.

I have applied the formula of Castle and Wright to the computation of the number of factor differences between *leucocephalus* and *albifrons*, and between *leucocephalus* and *polionotus* respectively in relation to both coloured area and red. The fact that, in these four cases, the numbers of factors indicated are 2 +, 2 −, 2 −, and 14 respectively, in itself shows that the formula is inapplicable here. Certain other methods which I have employed have likewise given impossibly small numbers of factors.

As indicating very limited numbers of factor differences, in some of these cases, we have pointed to the relatively large proportion of seemingly pure segregants for both of the chief indices of pigmentation (coloured area and red), in the *leucocephalus-albifrons* cross, and for coloured area, in the *leucocephalus-polionotus* cross. The numbers here indicated range, for the most part, from two to four.

Against such a limited number of factor differences we have, however, a much greater array of evidence. We may mention here (1) the comparatively symmetrical distribution of values in the second backcross with *leucocephalus*; (2) the occurrence, within each sub-species, of genetic differences in respect to all of the characters, each of these minor differences being dependent upon multiple factors if this theory be accepted; (3) the existence, within both *albifrons* and *polionotus*, of geographically graded differences, some of which, at least, are known to be genetic and to depend upon more than one factor.

One means of escape from this dilemma readily suggests itself. May not the differences between the distinct sub-species be due to a relatively small number of major factors, while the local differences within a sub-species, or the differences within a single population, are due to a considerable number of minor, "modifying," factors? If the "major" factors be supposed to far outweigh the "minor" ones in their quanti-

tative effects, a segregant which was "pure" for all the major factors of one sub-species might reach or surpass the mean value of that sub-species, in respect to a given character, even though it was not pure for all the minor factors, which entered the cross.

It would be difficult, however, to account, on such a basis, for the approximately symmetrical distribution of the "7/8 *leucocephalus*" populations, already discussed at some length. If we had to do with three or four factors, capable of producing the major pelage differences between *leucocephalus* and *polionotus*, the presence of even a large number of modifying factors, of the sort which might be supposed to underly the minor individual differences, would not suffice to mask the asymmetry to be expected in a histogram based upon such material. Moreover, it would seem more probable, on the basis of the multiple factor hypothesis, that the differences between two sub-species would depend upon a greater number of factors, instead of upon more potent factors, than the difference between two individuals within a sub-species. For presumably the sub-specific differences have arisen through the accumulation of the same type of genetic differences as distinguish members of the same sub-species.

If we are to retain the multiple factor interpretation at all, it seems to me that we must attribute any one of the sub-specific differences here considered to a much greater number of factors than three or four. This means that there is something wrong with the argument based upon the number of apparently "pure" segregants. Our argument contained the implicit assumption that all of the allelomorphs tending to increase the degree of pigmentation (to raise the value of A and to lower the value of R) were contained in one of the two sub-species entering a cross, while all of the allelomorphs tending to decrease the degree of pigmentation were contained in the other. But this, of course, is not necessarily true. *Leucocephalus*, for example, might have the constitution *aabbccddeeFF*, in respect to a given character difference, while *albifrons* had the constitution *AABBCCDDEEff*. In such an event, it is plain that the chance that an F_2 individual would equal or exceed one or the other of the parent races would be very much greater than if all of the "lower case" genes were on one side, and all the "capitals" on the other. For it would not be necessary, in order to reach this level of darkness or pallor, that an individual should be homozygous for all of the factors derived from either race[1]. A marked asymmetry of distribution in the

[1] I am here leaving out of account the part played by the phenotypic variability of each single genotype. It has been assumed above (p. 296) that the chance for an incomplete segregant to reach or exceed the mean value of a given parent race would be balanced by the chance that a pure segregant should fall below this level.

second back-cross would remain, however, even upon the foregoing assumption.

Formally, at least, we have thus reconciled our conflicting evidence by an interpretation which is quite in harmony with the multiple factor hypothesis. While such an interpretation is far from being proved, at the present time, I know of no other which fits the facts as well.

A yet more interesting problem is that of the nature of the genetic connection between certain components of the sub-specific complex of characters. I have previously called attention to the fact that high correlations among the various pigmental characters may be observed, when series of contiguous races are thrown together and treated as single populations, whereas correlations between the same pairs of characters are found to be much weaker, or even to be imperceptible, when the component collections are treated separately[1]. I have given reasons for believing that this higher degree of inter-racial correlation, as compared with intra-racial, is due to the fact that the mean differences between the local races are entirely genetic, whereas the individual differences within any single race are partly phenotypic, *i.e.* non-hereditary. That there is some sort of a close genetic bond among the various racial differences in pigmentation has already been fully shown. The non-hereditary modifications of these characters (however produced) appear, on the contrary, to be largely independent of one another. In the case of certain other characters, to be sure (*e.g.* tail and foot), environmental influences (temperature, nutrition) are known to bring about parallel modification, but there is no indication that the various pigmental characters here considered are subject to coincident changes of this sort during the individual lifetime. Unfortunately, the nature of the non-hereditary fraction of all individual variability in animals is a subject concerning which, at the present time, we are very largely in the dark.

The interesting relations narrated in paragraph 23 of the foregoing summary are open to a similar interpretation. The higher degree of correlation among these characters which is found in the F_2 generation, as compared with the F_1, is due to an increase in the proportion of the total variability which is genetic, combined with the fact that the characters are in some way bound together genetically[2].

[1] Sumner (1929 *a*). See also Bubnoff (1919).

[2] It is probably needless to say that the larger coefficients found in the F_2 generation do not result from a mere increase in the range of variation of the correlated characters. The standard deviations are of course increased, as well as the product moments.

The still further increase in these correlations which is manifested in the F_3 generation is due to the procedure adopted in the selection and mating of the parents. The more extreme segregants which were selected as "pale" and "dark" constituted about two-thirds of those thus chosen. This circumstance, and the further fact that at least two pigmental characters were taken into account in making the choice would inevitably result in high correlations among this parent group when treated as a single population[1]. And since these latter were mated assortatively (pale with pale, etc.), a similar genetic constitution was reflected in the F_3 generation.

Regarding the nature of this genetic connection among our correlated characters, two hypotheses are possible: (1) The characters in question may be merely different manifestations of the same genetic factors (*e.g.* the extent of both tail stripe and coloured area may depend upon factors which determine the amount of pigmented hair upon the tail and trunk alike). (2) The factors underlying these characters may be more or less closely linked, due to their presence in the same chromosome. And it is of course possible that each of these explanations may be true in part. On the other hand, parallel modification, through environmental influences acting during ontogeny, could hardly account for correlations which increase as a result of segregation.

While the data thus far discussed lend themselves perhaps equally well to either of the foregoing interpretations, there is one circumstance which strongly favours the hypothesis that our correlations result from the various pigmental characters being determined in part by a genetic basis common to all of them. I refer to the frequent association between intensity and extensity of pigmentation, upon various parts of the body, and in animals belonging to widely different groups. This phenomenon is so well known to students of systematic ornithology and mammalogy that it need not be discussed here. Reference need only be made to the diminution both in the intensity and extensity of coloured areas in desert species, as compared with the denizens of more humid climates (Allen, 1906; Buxton, 1923; Görnitz, 1923; Sumner, 1925; Rensch, 1929). In connection with this class of facts, the hypotheses of linkage can hardly be invoked as an explanation. For studies of linkage thus far

[1] As a matter of fact the correlations in these groups of selected parents were probably at least as high as in their F_3 offspring. Thus, in the *leucocephalus-albifrons* series, the correlation between A_b and R among the selected F_2 parents was $-0{\cdot}912$, that of their offspring $-0{\cdot}788$. Similar figures for the *leucocephalus-polionotus* cross (in this case, A_t and R) are $-0{\cdot}822$ and $-0{\cdot}858$ respectively. In both cases the deviations of each parent have been weighted by the number of offspring.

made have surely revealed no general tendency toward the close propinquity, within the same chromosome, of genes which bring about similar physiological or morphological conditions. On the contrary, their associations with one another are on the whole surprisingly haphazard and arbitrary.

That each of these characters, on the other hand, is partially determined by independent genetic factors will be rendered equally probable by the evidence. The fact that the correlated characters under consideration all have a considerable range of independent variability—to such a degree, indeed, that the coefficients are sometimes reduced to zero—does not, of course, prove the case as regards independent *genetic* variability. Much of the variability of all organisms is known to be "phenotypic" or "somatic"—whatever that means. At least, much of it is not transmissible, as is shown by the low values of most parent-offspring correlations.

Of more evidential value, in this connection, are certain relations which appear in comparing one race with another. Attention has already been called to a curious anomaly presented by the Foster's Bank collection of *albifrons*. This local sub-race is at once *darker* and possessed of a *smaller* coloured area and *shorter* tail stripe (reduced to 0 in most cases) than are the other representatives of *albifrons* found near the coast. Although the collection is unfortunately small (twenty specimens) the differences in these respects are so considerable and so constant that they very probably represent actual differences in the respective local populations. Moreover, the differences revealed by the sample collected prove to be genetic ones (Text-figs. 3, 10). These facts speak for the partial genetic independence of the characters concerned, despite the fact that "red" is, in general, negatively correlated with the other two characters, both within single populations, and particularly when we consider a series of such populations in geographic sequence.

Once more, identical coloured areas are associated with different values for red in different racial crosses[1]. Thus, if we compare individuals with the same value for coloured area, in the 3/4 *albifrons* and 3/4 *polionotus* series respectively of the *polionotus-albifrons* cross, we find that the value for red is much higher in the former than in the latter, *i.e.* the former are paler.

But still more important light upon this subject is derived from an application of the method of partial correlation. The correlation between

[1] Pure races cannot be directly compared for this purpose, since there is practically no overlap in respect to the values for either of these characters.

the two measurements of the coloured area ("base" and "tips") is high in all of the groups for which both values have been determined. It approaches unity in the F_2 and F_3 generations of the *leucocephalus-polionotus* cross. It may nevertheless be shown by the method referred to that "red" is correlated to some extent with each of these determinations of coloured area, independently of the other. For East Pass *albifrons*, the mean of these two "net" coefficients is − 0·210; for the F_2 generation of *leucocephalus-polionotus* hybrids the mean is − 0·177; for the F_3 generation it is − 0·235. All of these six values are of the same sign. The aggregate number of individuals on which they are based is 230. In the F_1 generation of this cross, on the other hand, one net coefficient is negative and the other positive, the mean being − 0·090.

The foregoing figures do not, of course, prove that this independent variability of the two measurements of coloured area is of the genetic sort. Unfortunately, this last question cannot be tested for these two characters, owing to circumstances which need not be detailed here. But the independent genetic variability of coloured area (either "base" or "tips") and red can be readily demonstrated. For this purpose, I have computed the parent-offspring correlations in respect to each of these characters, when the influence of the other has been eliminated. I have confined my computations to those generations between which correlation was found to be highest, namely, the F_2 and F_3 generations of both the *leucocephalus-albifrons* and the *leucocephalus-polionotus* crosses. As has already been pointed out, the amount of genetic variation in these F_3 generations and in the selected groups of F_2 parents is extremely high.

	Leucocephalus-albifrons F_2–F_3				*Leucocephalus-polionotus* F_2–F_3			
Character	No. of parents*	No. of off-spring	r (gross)	r (net)	No. of parents*	No. of off-spring	r (gross)	r (net)
A	22	65	+0·751	+0·344	26	82	+0·917	+0·712
R	22	65	+0·743	+0·437	24	82	+0·837	+0·464

* Here and elsewhere, in computing parent-offspring correlations, each parental deviation has been repeated to correspond with the number of offspring. Each filial deviation has thus been paired off against a parental one, and the n of the formula has been the number of offspring, rather than that of the parents. A similar weighting process was applied in computation of means and standard deviations in these cases. This procedure has both advantages and disadvantages.

In computing the net parent-offspring correlation for coloured area, the influence of red being eliminated, the three gross coefficients used were (1) that for coloured area (parents) and coloured area (offspring),

(2) that for coloured area (parents) and red (parents), and (3) that for red (parents) and coloured area (offspring). Conversely, in computing the net parent-offspring correlation for red, the gross coefficients used were those for red (parents) and red (offspring), coloured area (parents) and red (parents), and coloured area (parents) and red (offspring). Four separate coefficients were computed for each series (fathers—sons, fathers—daughters, mothers—sons, mothers—daughters). The weighted mean of these four figures, for each cross and each character, is given above.

It will be seen that these "net" coefficients are from a half to three-quarters as great as the "gross" ones. This can only be interpreted as showing that a large proportion of the variation which each of these characters undergoes, independently of the other, in this material at least, is genetic.

It is relevant to call attention, likewise, to the relatively high values of the cross-correlations, computed at this time, as compared with the direct ones. Thus, the weighted mean of the four cross-correlations here considered (coloured area of parents with red of offspring, and *vice-versa*, in the two crosses) is $-0{\cdot}767$, the weighted mean of the direct correlations being $+0{\cdot}819$. We may also refer again to the striking correlations (Text-fig. 13) between coloured area, in the *leucocephalus* parents, and tail stripe in the F_1 generation of a cross with *polionotus*, despite the fact that tail stripe itself is totally lacking in the former race.

To sum up our conclusions from the facts discussed in the last few paragraphs, we may say that the close correlation found to exist between certain pigmental characters is probably due to their partial dependence upon common genetic factors. That the correlation is never absolute is due in part to the existence of independent factors which influence one character without affecting the other; in part to the presence of a considerable degree of non-genetic variability. It is possible that linkage likewise exists here and further complicates the situation. But it is not necessary to assume its occurrence.

This is quite a different conclusion from that of Tine Tammes (1912) in the case of flax hybrids. This author attributes the correlation of certain characters in the F_2 generation to linkage ("in the gamete formation in the F_1 particular factor combinations occur by preference"), although it is stated that these correlations are already feebly present in the F_1 and the parent races. She is led to the rather surprising conclusion "that a closer interdependence exists between the factor groups for the various characters than between the factors for the same cha-

racter." Such a situation might be intelligible on the basis of polyploidy, but it is, at best, entirely hypothetical.

Whatever may be the situation in respect to flax, I regard such an explanation as much less satisfactory for *Peromyscus* than that of the multiple effects of the same genes. In this respect, my interpretation is in accord with that of Dobzhansky (1927), who adopts the hypothesis of "multiple effects," rather than that of linkage, in explaining the correlation between the pigmentation of the eye and that of the testis in *Drosophila*. In the case described by Dobzhansky, however, the correlation is absolute, and seems to depend upon a single pair of allelomorphs. Moreover, the pigmentation of certain other regions of the body is quite independent of that of the parts named. These last statements do not appear to hold for any of the sub-specific differences with which I have dealt in the case of *Peromyscus*, though they apply, one or all, to certain colour mutations which I have described in species of this genus (Sumner, 1917, 1928; Sumner and Collins, 1922).

The foregoing interpretation is offered only for the correlations between one pigmental character and another. A few further words are necessary regarding another type of correlation which has been discussed above, namely, that between foot or tail length, on the one hand, and the various pigmental characters on the other. The evidence for such correlation has been discussed in detail in connection with each of the three sub-specific crosses considered in the present paper, and it need not be repeated here. Statistically, the case is strong that this series of coincidences does not result from random sampling.

Certain circumstances have already been mentioned which considerably weaken the conclusion that the preponderant occurrence in some of the segregating generations, of coefficients having the "expected" sign, is due to any genetic bond between the two classes of characters. I refer especially to (1) the fact that the standard deviations for foot and tail length are not preponderantly greater in the F_2 generation than in the F_1; and (2) the related fact that the correlations between tail and foot length show no constant tendency to be greater in the F_2 and F_3 generations than in the F_1 hybrids and the pure races. So far as they go, these last facts are not in accord with the supposition that there is any manifest segregation of the genetic factors which underly racial differences in the length of these two members. Yet the correlations referred to in the preceding paragraph would seem to depend upon the simultaneous segregation of factors affecting the length of the latter and ones affecting pigmental characters.

Let us assume, however, that these corelation have an actual

genetic basis, and that they result from a tendency of certain racial characters to segregate in their original combinations[1]. I believe that in that case the hypothesis of linkage, rather than that of multiple effects of the same genes, would be preferable. For, in the first place, the correlations are so feeble that in most instances they are statistically non-significant, when taken singly; and in the second place, the length of tail and foot bears no general relation, in this genus as a whole, to the extent or shade of the coloured area of the pelage. In a recent paper (1929) I have pointed out that while the *albifrons* of the immediate neighbourhood of the coast has a markedly longer tail and foot than *polionotus*, we meet with a type, only 20 miles inland, in which these members are no longer than in the latter race. Furthermore, on the Pacific coast, it is the *darkest* sub-species of *Peromyscus maniculatus* that have by far the *longest* tails and feet, and this reversed association holds throughout a considerable area. This last fact, as well as the exactly opposite relation of these same characters in certain members of the *P. polionotus* series[2] could both be accounted for on the basis of a rather low degree of linkage between some of the factors concerned[3].

A few words, in conclusion, relative to the bearing of these studies upon our conceptions of the process of evolution. It is evident that in no case does one of these sub-species, or even a genetically distinct subdivision of such a sub-species, appear to have arisen through a single act of mutation. Wherever investigated, such races or sub-races appear to differ by considerable numbers of Mendelian factors. Since these differences have frequently been accumulated in a fairly consistent manner, along some geographic, climatic or edaphic gradient, we can hardly regard the relationships as being entirely haphazard ones[4]. Either

[1] These phenomena may be related to certain evidences for the coherence of specific characters which were obtained by Gates (1925) in crossing *Mus musculus* with the Japanese waltzing-mouse, and which were interpreted by him on the assumption that "the chromosomes of each species tend to segregate as a group and not at random."

[2] *Leucocephalus*, coast *albifrons*, and *polionotus* represent a series of decreasing tail and foot length, and of increasing pigmentation.

[3] However, it is worth noting that a recent examination of measurements from the F_2 generation of certain sub-specific crosses of *P. maniculatus* discussed in an earlier paper (Sumner, 1923 *a*) has revealed no consistent tendency toward correlations of the sort here considered.

[4] This subject has been discussed in an illuminating manner in two recent volumes (Robson, 1928; Rensch, 1929), while Osborn (1927 and earlier papers) has brought together much valuable material, and made this the basis of an interesting theoretical discussion. I have myself considered certain of these cases of intergradation in some detail (Sumner, 1923, 1929, 1929 *a*).

(1) there has been a selection on the basis of adaptedness (whether in respect to the visible manifestation of these factors or to some more recondite effects); or (2) the genetic changes have resulted in some more direct way, from the action of the environment. In various earlier papers I have argued for the second of these alternatives[1], and I still believe that it is the more probable one in many instances, particularly in those cases in which humidity and aridity appear to have been the controlling factors. It must be admitted, however, that the simultaneous transformation of considerable series of pigmental characters, even when these are but feebly correlated within any single population, is not, in itself, to be regarded as evidence of their parallel modification by the environment, as I formerly supposed. This becomes obvious if we accept the conclusion that these characters rest, in part, upon a common genetic basis.

In the case of the present series (*polionotus-albifrons-leucocephalus*), it seems much more likely that an important element in the situation has been a selective effect of the environment, on the basis of colour. As regards the pigmental changes, the admittedly ill-supported, though far from disproved theory of "concealing coloration" seems to fit these facts better than any other[2].

Such an interpretation does not mean, however, that the actual factorial changes or "mutations" have necessarily occurred at the time when one geographic race has arisen from another. There is much genetic diversity in every natural population, resulting presumably from factorial changes which have occurred in the past, combined with hybridisation in the broadest sense of the term. It is likely, therefore, that rather wide divergence could be brought about in such a population by continued selection, in the entire absence of new mutations. If it should turn out that suitable mutations likewise occur from time to time, and particularly if such mutations are in any way responsive to organic "needs," the process would, of course, be vastly expedited. Or appropriate crosses between different existing stocks might give rise to an adequate supply of variations, as Lotsy and others have so forcefully contended.

I trust, however, that the foregoing remarks will not be taken to imply that I regard such a "mutational" explanation of the origin of these geographic races, or of species in general, as either adequate or satisfying. It is no more adequate or satisfying than is the related notion that the entire heritage of an organism consists of an aggregation of Mendelian genes. Both conceptions, I believe, are to be viewed merely

[1] Sumner (1920, 1923, 1925). [2] Sumner (1929, 1929 *a*).

as highly useful provision hypotheses, which account for certain important aspects of individual and racial development, but which entirely overlook certain others. In this belief I think it likely that I am in agreement with many mutationists, though probably not with all.

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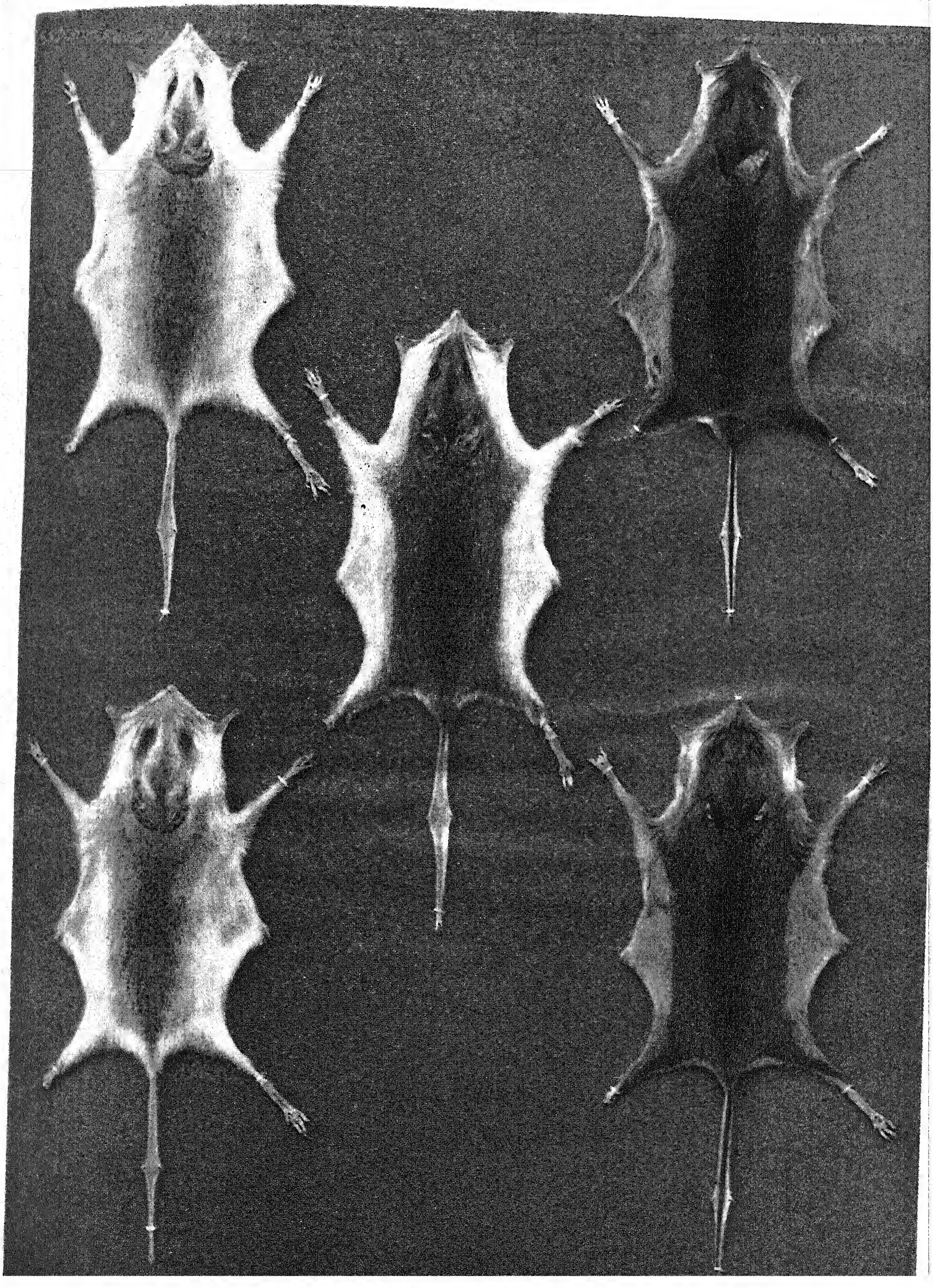
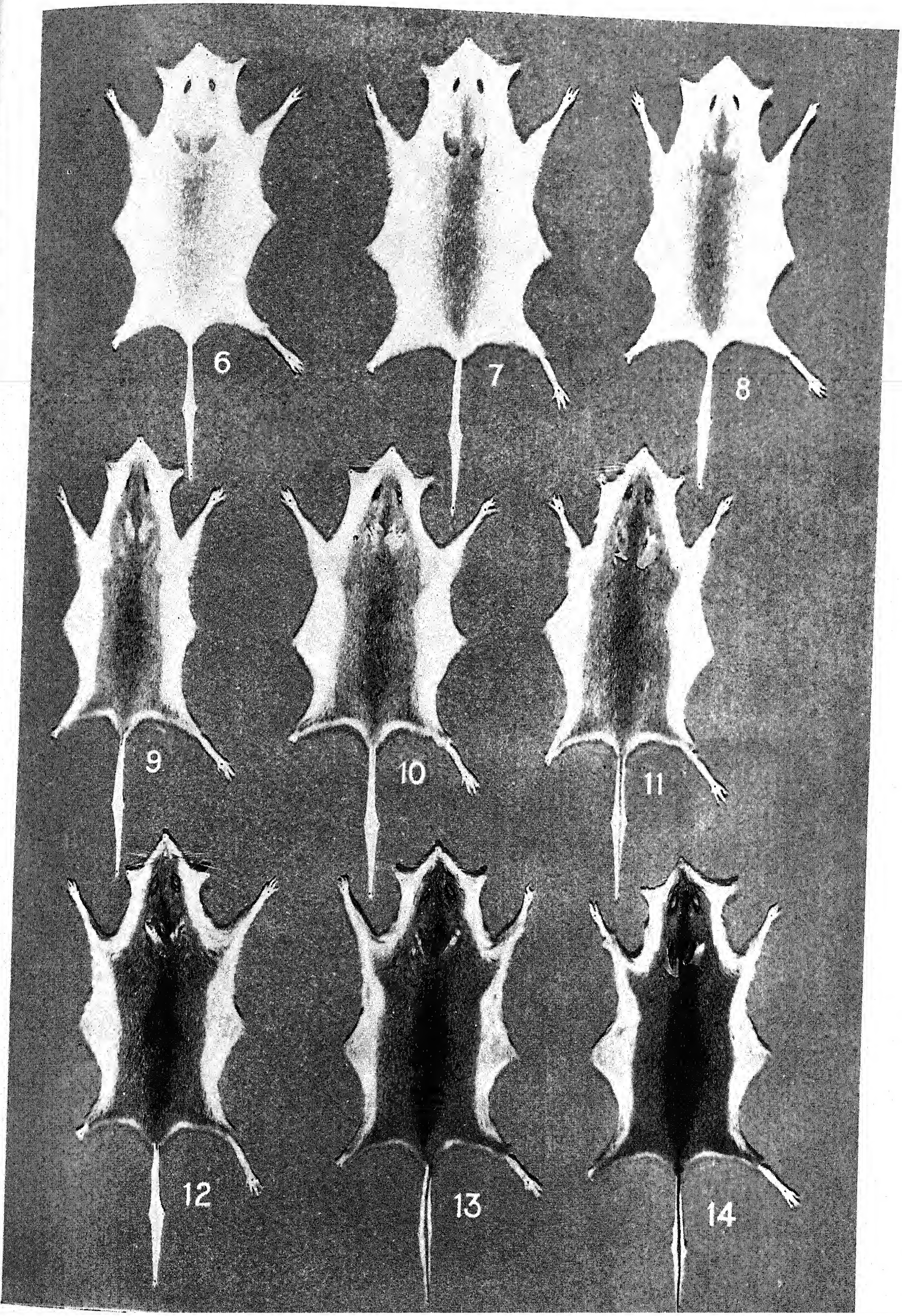
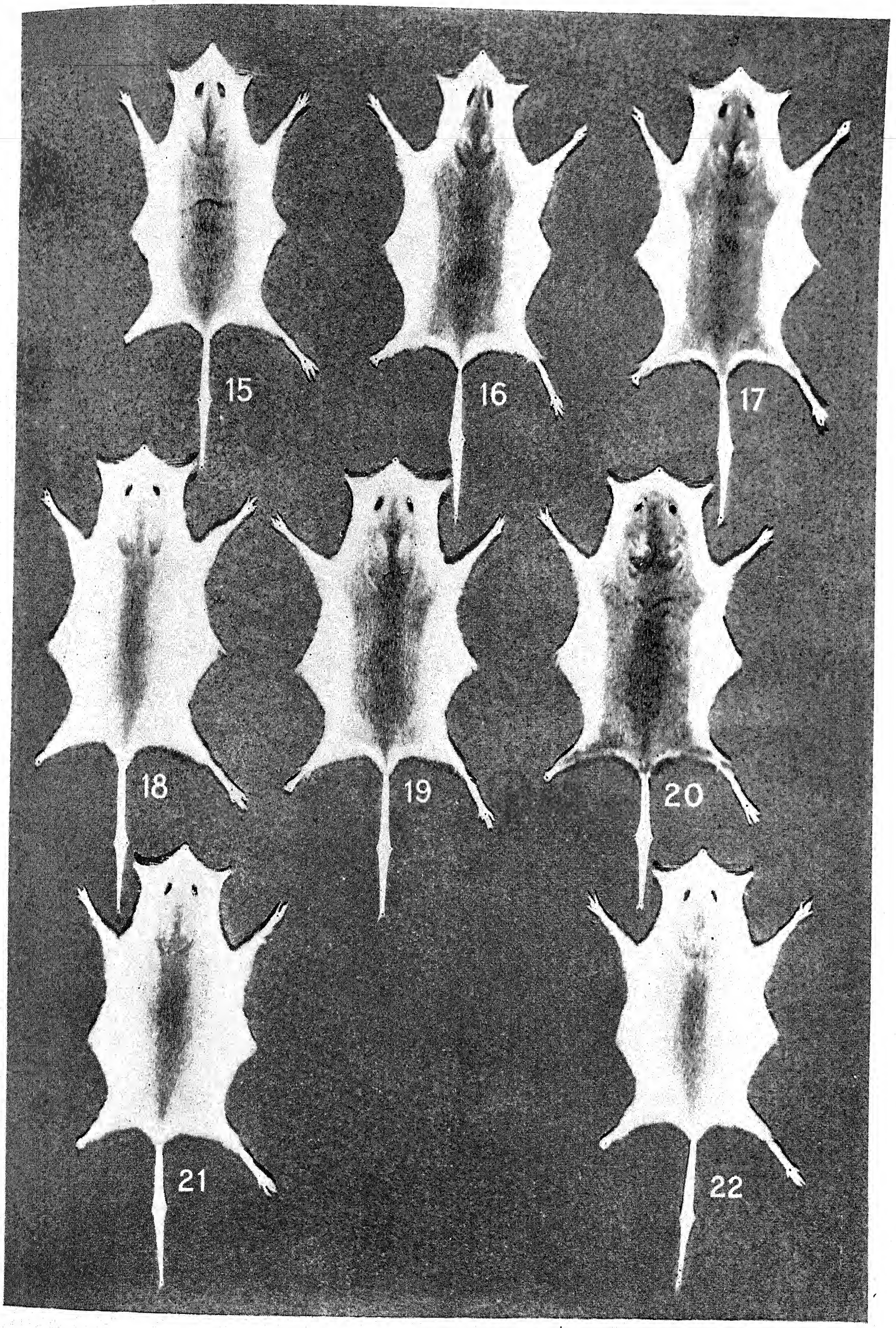


PLATE IX

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EXPLANATION OF PLATES VIII—XI.

PLATE VIII.

Fig. 1. (Upper left.) Skin of *Peromyscus polionotus leucocephalus*, close to average in respect to all pelage characters.

Fig. 2. (Centre.) Average *P. p. albifrons* (East Pass series).

Fig. 3. (Upper right.) Average *P. p. polionotus* (Autaugaville series).

Fig. 4. (Lower left.) Extreme pale segregant in F_2 generation of *leucocephalus-polionotus* (*i.e.* cross between sub-species *leucocephalus* and *polionotus*).

Fig. 5. (Lower right.) Extreme dark segregant in F_2 generation of same cross.

PLATE IX.

Figs. 6, 7, 8. Palest, mean and darkest specimens of *leucocephalus*. In choosing extremes, here and elsewhere, the values both for "coloured area" and "red" were taken into consideration, and a skin was chosen, in each case, which gave nearly or quite the extreme values for both of these characters. (The actual extreme values are not always combined in the same individual.) In choosing the means, "coloured area," "red," and the "index of saturation" were all taken into account.

Figs. 9, 10, 11. Palest, mean and darkest skins of *albifrons* (East Pass series).

Figs. 12, 13, 14. Palest, mean and darkest skins of *polionotus*.

PLATE X.

Figs. 15, 16, 17. Palest, mean and darkest specimens in F_1 generation of *leucocephalus-albifrons* cross.

Figs. 18, 19, 20. Palest, mean and darkest specimens in F_2 generation of same cross.

Fig. 21. Palest specimen in first back-cross with *leucocephalus* (3/4 *leucocephalus*).

Fig. 22. Palest specimen in second back-cross with *leucocephalus* (7/8 *leucocephalus*).

PLATE XI.

Figs. 23, 24, 25. Palest, mean and darkest specimens in F_1 generation of *leucocephalus-polionotus* cross.

Figs. 26, 27, 28. Palest, mean and darkest specimens in F_2 generation of same cross.

Fig. 29. Palest specimen in first back-cross with *leucocephalus* (3/4 *leucocephalus*).

Fig. 30. Palest specimen in second back-cross with *leucocephalus* (7/8 *leucocephalus*).

TABLE

Mean values, Leucocephalus,

	Sex	*Leucocephalus* Wild	*Leucocephalus* Parents of F_1*	*Leucocephalus* C_1	*Albifrons* East Pass	*Albifrons* Parents of F_1*	*Albifrons* Foster's Bank	*Albifrons* Ono Island	*Albifrons* C_1 generation (combined)	F_1 (East Pass derivatives only) All	F_1 (East Pass derivatives only) Parents of F_1*
umber ...		72 (33♂, 39♀)		46 (27♂, 19♀)	41 (25♂, 16♀)		21 (16♂, 5♀)	16 (4♂, 12♀)	50 (30♂, 20♀)	59 (31♂, 28♀)	
y length	♂	77·79 ± 0·24	—	77·67 ± 0·26	78·84 ± 0·27	—	78·50	78·75	78·48 ± 0·21	77·92 ± 0·21	—
	♀	82·29 ± 0·36	—	81·37 ± 0·45	83·12 ± 0·47	—	82·40	82·46	80·27 ± 0·44	81·82 ± 0·34	—
length	Both	54·21 ± 0·20	—	51·42 ± 0·25	53·49 ± 0·34	—	52·37	55·37	52·35 ± 0·27	53·24 ± 0·24	—
tual)	♂	53·27 ± 0·24	—	50·24 ± 0·22	52·48 ± 0·41	—	—	—	51·71 ± 0·31	52·23 ± 0·31	—
	♀	55·03 ± 0·27	—	53·11 ± 0·40	55·06 ± 0·47	—	—	—	53·27 ± 0·46	54·36 ± 0·32	—
rrected)†	♂	54·24	—	51·26	52·99	—	—	—	52·38	53·14	—
	♀	53·93	—	52·46	53·58	—	—	—	53·14	53·50	—
t length	♂	18·52 ± 0·04	—	18·49 ± 0·05	17·74 ± 0·05	—	18·15	18·37	17·69 ± 0·05	18·12 ± 0·05	—
tual)	♀	18·50 ± 0·05	—	18·44 ± 0·04	17·78 ± 0·07	—	18·25	18·15	17·67 ± 0·07	18·13 ± 0·09	—
rrected)	♂	18·70	—	18·68	17·84	—	18·21	18·43	17·82	18·29	—
	♀	18·34	—	18·34	17·56	—	18·08	17·97	17·65	18·00	—
length	Both	14·50 ± 0·04	—	14·04 ± 0·04	14·72 ± 0·06	—	14·63	14·34	14·81 ± 0·06	14·47 ± 0·04	—
tual)	♂	14·27 ± 0·05	—	14·01 ± 0·06	14·58 ± 0·07	—	—	—	14·62 ± 0·07	14·45 ± 0·06	—
	♀	14·68 ± 0·05	—	14·08 ± 0·06	14·93 ± 0·08	—	—	—	15·08 ± 0·10	14·50 ± 0·06	—
rrected)	♂	14·42	—	14·17	14·66	—	—	—	14·72	14·59	—
	♀	14·57	—	14·01	14·78	—	—	—	15·07	14·41	—
ght	♂	12·72 ± 0·17	—	12·64 ± 0·20	13·00 ± 0·19	—	—	—	12·66 ± 0·19	12·80 ± 0·13	—
	♀	13·00 ± 0·17	—	12·54 ± 0·26	12·45 ± 0·17	—	—	—	11·96 ± 0·26	14·03 ± 0·20	—
ìal tebrae	Both	23·46 ± 0·05	—	—	24·56 ± 0·09	—	23·88	—	—	23·60 ± 0·06	—
ıt pelvis	♂	14·53 ± 0·05	—	—	15·11 ± 0·05	—	—	—	—	14·61 ± 0·05	—
tual)	♀	15·43 ± 0·07	—	—	15·79 ± 0·09	—	—	—	—	15·35 ± 0·08	—
rrected)	♂	14·84	—	—	15·27	—	—	—	—	14·90	—
	♀	14·99	—	—	15·19	—	—	—	—	15·00	—
ıt femur	♂	14·06 ± 0·04	—	—	13·99 ± 0·05	—	—	—	—	13·81 ± 0·04	—
tual)	♀	14·79 ± 0·06	—	—	14·82 ± 0·09	—	—	—	—	14·51 ± 0·07	—
rrected)	♂	14·34	—	—	14·14	—	—	—	—	14·08	—
	♀	14·36	—	—	14·23	—	—	—	—	14·17	—
l length	♂	22·88 ± 0·05	—	—	22·63 ± 0·05	—	—	—	—	22·61 ± 0·06	—
tual)	♀	23·21 ± 0·05	—	—	22·89 ± 0·07	—	—	—	—	23·03 ± 0·07	—
rrected)	♂	23·24	—	—	22·82	—	—	—	—	22·94	—
	♀	22·88	—	—	22·44	—	—	—	—	22·77	—
l breadth	♂	10·01 ± 0·02	—	—	10·05 ± 0·03	—	—	—	—	9·99 ± 0·02	—
tual)	♀	10·03 ± 0·02	—	—	9·99 ± 0·02	—	—	—	—	10·12 ± 0·02	—
stripe	Both	0	—	0	41·73	40·74	0·81	38·37	31·31	3·81	4·29
; pigment	Both	0	—	0	0·07	—	0	0·29	—	0·23	—
ured area	Both	45·54 ± 0·32	43·66	43·80 ± 0·34	66·46 ± 0·33	67·12	56·80	72·87	61·74 ± 0·59	56·24 ± 0·26	56·04
se)	♂	45·21 ± 0·46	—	42·96 ± 0·42	66·39 ± 0·42	—	—	—	61·90 ± 0·83	56·09 ± 0·38	—
	♀	45·81 ± 0·44	—	44·81 ± 0·52	66·56 ± 0·53	—	—	—	61·50 ± 0·76	56·41 ± 0·34	—
ured area	Both	—	—	—	59·79 ± 0·54	60·51	47·95	65·47	—	—	—
ɔs)	♂	—	—	—	59·56 ± 0·71	—	—	—	—	—	—
	♀	—	—	—	60·12 ± 0·82	—	—	—	—	—	—
	Both	25·40 ± 0·30	26·03	27·66 ± 0·42	17·17 ± 0·15	16·84	15·07	14·51	16·99 ± 0·13	19·32 ± 0·13	19·14
	♂	26·05 ± 0·45	—	28·01 ± 0·57	17·39 ± 0·17	—	—	—	17·15 ± 0·18	19·74 ± 0·18	—
	♀	24·90 ± 0·39	—	27·26 ± 0·61	16·86 ± 0·26	—	—	—	16·75 ± 0·17	18·85 ± 0·15	—
	Both	1·82 ± 0·02	1·71	1·63 ± 0·03	3·90 ± 0·03	3·95	3·81	5·05	3·66 ± 0·05	2·93 ± 0·03	2·93
$\underline{V}$	Both	27·66 ± 0·41	23·84	25·96 ± 0·50	42·02 ± 0·54	39·04	37·60	30·73	36·22 ± 0·57	35·90 ± 0·37	33·97

* Weighted by number of offspring.

I.

Albifrons *and hybrids.*

F_2 (East Pass derivatives only) 75 (35♂, 40♀)	Back-cross: 3/4 *leucocephalus* (East Pass derivatives only) 58 (35♂, 23♀)	Back-cross: 3/4 *albifrons*	Grades: 7/8 *leucocephalus* (East Pass derivatives only) 41 (19♂, 22♀)	Selected parents of F_3 (weighted by number of offspring): Pale	Selected parents of F_3: Medium	Selected parents of F_3: Dark	F_3: All 65 (41♂, 24♀)	F_3: Pale 17 (12♂, 5♀)	F_3: Medium 27 (17♂, 10♀)	F_3: Dark 21 (12♂, 9♀)
78·11 ± 0·24	78·69 ± 0·19	—	77·47 ± 0·32	—	—	—	78·48 ± 0·16	78·25	78·32	78·92
81·11 ± 0·26	80·83 ± 0·28	—	78·77 ± 0·18	—	—	—	81·46 ± 0·21	81·60	81·65	81·17
53·09 ± 0·21	52·35 ± 0·22	52·93	52·54 ± 0·16	—	—	—	53·73 ± 0·15	53·50	52·91	54·98
52·69 ± 0·26	51·89 ± 0·27	—	51·97 ± 0·26	—	—	—	53·39 ± 0·18	53·50	52·59	54·42
53·44 ± 0·32	53·06 ± 0·34	—	53·02 ± 0·18	—	—	—	54·31 ± 0·25	53·50	53·45	55·72
53·52	52·47	—	53·08	—	—	—	54·06	—	—	—
52·91	52·67	—	53·60	—	—	—	53·62	—	—	—
18·28 ± 0·05	18·42 ± 0·04	18·01	18·42 ± 0·05	—	—	—	18·37 ± 0·04	18·54	18·27	18·35
18·00 ± 0·05	18·23 ± 0·06	17·80	18·27 ± 0·05	—	—	—	18·19 ± 0·04	18·48	18·12	18·11
18·43	18·53	—	18·63	—	—	—	18·50	—	—	—
17·93	18·17	—	18·36	—	—	—	18·09	—	—	—
14·41 ± 0·03	14·35 ± 0·03	14·42	14·20 ± 0·04	—	—	—	14·48 ± 0·04	—	—	—
14·43 ± 0·05	14·41 ± 0·04	—	14·20 ± 0·05	—	—	—	14·50 ± 0·05	—	—	—
14·39 ± 0·04	14·27 ± 0·05	—	14·20 ± 0·07	—	—	—	14·47 ± 0·07	—	—	—
14·56	14·50	—	14·37	—	—	—	14·60	—	—	—
14·33	14·23	—	14·26	—	—	—	14·40	—	—	—
12·73 ± 0·15	13·10 ± 0·17	—	12·40 ± 0·23	—	—	—	12·67 ± 0·18	11·37	12·91	13·63
13·32 ± 0·16	12·49 ± 0·15	—	12·18 ± 0·19	—	—	—	12·67 ± 0·17	12·14	12·57	13·09
23·67 ± 0·07	—	—	—	—	—	—	—	—	—	—
14·49 ± 0·05	—	—	—	—	—	—	—	—	—	—
15·16 ± 0·06	—	—	—	—	—	—	—	—	—	—
14·75		—	—	—	—	—	—	—	—	—
14·95	—	—	—	—	—	—	—	—	—	—
13·74 ± 0·05	—	—	—	—	—	—	—	—	—	—
14·29 ± 0·06	—	—	—	—	—	—	—	—	—	
13·98	—	—	—	—	—	—	—	—	—	—
14·08	—	—	—	—	—	—	—	—	—	—
22·70 ± 0·05	—	—	—	—	—	—	—	—	—	—
22·86 ± 0·05	—	—	—	—	—	—	—	—	—	—
23·00	—	—	—	—	—	—	—	—	—	—
22·70	—	—	—	—	—	—	—	—	—	—
9·98 ± 0·02	—	—	—	—	—	—	—	—	—	—
10·03 ± 0·02	—	—	—	—	—	—	—	—	—	—
9·33	1·22	14·33	0·05	0	2·33	42·31	21·23	0·82	8·48	54·14
0·28	0·22	0·80	0·12	—	—	—	0·15	—	—	—
57·18 ± 0·45	51·64 ± 0·41	61·27	48·00 ± 0·45	46·91	55·80	63·02	56·62 ± 0·61	47·82	56·81	63·48
57·11 ± 0·56	51·51 ± 0·59	—	48·21 ± 0·57	—	—	—	55·95 ± 0·78	47·67	57·06	62·67
57·23 ± 0·70	51·83 ± 0·52	—	47·82 ± 0·68	—	—	—	57·75 ± 0·99	48·20	56·40	64·56
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
20·66 ± 0·20	23·40 ± 0·26	19·07	25·17 ± 0·33	24·70	20·63	16·73	20·95 ± 0·28	24·66	20·67	18·31
20·93 ± 0·26	23·60 ± 0·34	—	24·98 ± 0·45	—	—	—	21·48 ± 0·37	25·16	21·01	18·46
20·41 ± 0·31	23·10 ± 0·42	—	25·34 ± 0·47	—	—	—	20·06 ± 0·37	23·48	20·11	18·11
2·82 ± 0·04	2·25 ± 0·04	—	1·93 ± 0·03	1·96	2·71	3·78	2·80 ± 0·06	2·01	2·78	3·50
35·94 ± 0·47	33·60 ± 0·39	38·53	30·85 ± 0·53	40·24	35·06	29·74	33·58 ± 0·55	40·94	31·59	30·19

† "Corrected" means are the "actual" ones, reduced to a standard body length of 80 mm.

TABLE II.

Mean values, Leucocephalus, Polionotus

	Sex	*Leucocephalus* Wild (all)	*Leucocephalus* Parents of F_1*	*Polionotus* Wild (all)	*Polionotus* Parents of F_1*	*Polionotus* C_1	F_1 All	F_1 Parents of F_2*	F_2 All	Back-cross 3/4 *leucocephalus*	Back-cross 3/4 *polionotus*	Grades 7/8 *leucocephalus*
umber ...		72 (33♂, 39♀)		46 (27♂, 19♀)		60 (39♂, 21♀)	74 (39♂, 35♀)		109 (56♂, 53♀)	67 (31♂, 36♀)	16 (10♂, 6♀)	55 (35♂, 20♀)
y length	♂	77·79 ± 0·24	—	78·59 ± 0·23	—	79·63 ± 0·22	78·05 ± 0·19	—	78·77 ± 0·21	78·97 ± 0·28	79·65	79·17 ± 0·20
	♀	82·29 ± 0·36	—	83·18 ± 0·58	—	83·83 ± 0·44	83·33 ± 0·35	—	81·42 ± 0·27	81·71 ± 0·33	81·60	80·75 ± 0·34
length	Both	54·21 ± 0·20	—	51·33 ± 0·32	—	51·64 ± 0·23	52·43 ± 0·23	—	52·84 ± 0·18	53·49 ± 0·18	51·93	53·69 ± 0·21
tual)	♂	53·27 ± 0·24	—	49·98 ± 0·31	—	50·71 ± 0·24	51·04 ± 0·25	—	52·11 ± 0·22	53·13 ± 0·24	51·80	53·51 ± 0·25
	♀	55·03 ± 0·27	—	53·28 ± 0·49	—	53·31 ± 0·39	53·97 ± 0·32	—	53·61 ± 0·28	53·81 ± 0·25	52·29	53·47 ± 0·37
rrected)†	♂	54·24	—	50·60	—	50·87	51·90	—	52·65	53·58	—	54·31
	♀	53·93	—	51·77	—	51·50	52·39	—	52·94	53·00	—	53·11
t length	♂	18·52 ± 0·04	—	17·31 ± 0·06	—	17·33 ± 0·04	17·95 ± 0·05	—	18·33 ± 0·05	18·46 ± 0·05	18·25	18·61 ± 0·04
tual)	♀	18·50 ± 0·05	—	17·25 ± 0·08	—	17·55 ± 0·07	17·94 ± 0·07	—	18·06 ± 0·05	18·32 ± 0·04	18·11	18·34 ± 0·06
rrected)	♂	18·70	—	17·42	—	17·36	18·11	—	18·43	18·55	—	18·76
	♀	18·34	—	17·03	—	17·28	17·70	—	17·96	18·20	—	18·29
length	Both	14·50 ± 0·04	—	15·01 ± 0·07	—	14·99 ± 0·04	14·61 ± 0·04	—	14·67 ± 0·03	14·53 ± 0·03	15·07	14·33 ± 0·03
tual)	♂	14·27 ± 0·05	—	14·93 ± 0·09	—	14·92 ± 0·05	14·60 ± 0·05	—	14·72 ± 0·05	14·41 ± 0·04	15·06	14·32 ± 0·04
	♀	14·68 ± 0·05	—	15·12 ± 0·10	—	15·13 ± 0·07	14·63 ± 0·05	—	14·60 ± 0·05	14·63 ± 0·04	15·09	14·35 ± 0·04
rrected)	♂	14·42	—	15·02	—	14·94	14·73	—	14·80	14·48	—	14·45
	♀	14·57	—	14·97	—	14·94	14·46	—	14·54	14·54	—	14·31
ght	♂	12·72 ± 0·17	—	12·33 ± 0·18	—	12·20 ± 0·20	12·21 ± 0·18	—	13·19 ± 0·16	13·32 ± 0·21	—	12·81 ± 0·15
	♀	13·00 ± 0·17	—	13·61 ± 0·38	—	14·15 ± 0·43	14·05 ± 0·25	—	13·33 ± 0·16	13·16 ± 0·20	—	13·15 ± 0·25
dal rtebrae	Both	23·46 ± 0·05	—	23·77 ± 0·08	—	—	23·51 ± 0·05	—	23·86 ± 0·05	—	—	—
ht pelvis	♂	14·53 ± 0·05	—	14·89 ± 0·07	—	—	14·57 ± 0·04	—	14·76 ± 0·05	—	—	—
ctual)	♀	15·43 ± 0·07	—	15·65 ± 0·09	—	—	15·41 ± 0·08	—	15·28 ± 0·06	—	—	—
orrected)	♂	14·84	—	15·09	—	—	14·84	—	14·93	—	—	—
	♀	14·99	—	15·04	—	—	14·77	—	15·01	—	—	—
ht femur	♂	14·06 ± 0·04	—	13·43 ± 0·07	—	—	13·64 ± 0·04	—	13·76 ± 0·04	—	—	—
ctual)	♀	14·79 ± 0·06	—	14·18 ± 0·12	—	—	14·27 ± 0·10	—	14·28 ± 0·05	—	—	—
orrected)	♂	14·34	—	13·61	—	—	13·89	—	13·92	—	—	—
	♀	14·36	—	13·58	—	—	13·64	—	14·01	—	—	—
ll length	♂	22·88 ± 0·05	—	22·70 ± 0·06	—	—	22·79 ± 0·05	—	22·87 ± 0·05	—	—	—
ctual)	♀	23·21 ± 0·05	—	23·04 ± 0·10	—	—	23·13 ± 0·07	—	23·03 ± 0·07	—	—	—
orrected)	♂	23·24	—	22·93	—	—	23·10	—	23·07	—	—	—
	♀	22·88	—	22·58	—	—	22·65	—	22·82	—	—	—
ll breadth	♂	10·01 ± 0·02	—	9·91 ± 0·03	—	—	9·98 ± 0·02	—	10·04 ± 0·02	—	—	—
ctual)	♀	10·03 ± 0·02	—	9·97 ± 0·05	—	—	10·05 ± 0·02	—	10·02 ± 0·02	—	—	—
l stripe	Both	0	—	100·00	—	—	18·29	18·81	26·05	2·04	45·19	1·40
ot pigment	Both	0	—	1·47 ± 0·08	—	1·97 ± 0·07	1·06 ± 0·07	—	0·83 ± 0·05	0·48 ± 0·05	1·75	0·31
oured area	Both	45·54 ± 0·32	44·99	—	—	—	68·33 ± 0·50	65·95	69·12 ± 0·90	55·05 ± 0·50	—	[illegible] ± 0·58
ase)	♂	45·21 ± 0·46	—	—	—	—	67·42 ± 0·68	—	66·45 ± 1·20	53·77 ± 0·59	—	[illegible] ± 0·75
	♀	45·81 ± 0·44	—	—	—	—	69·33 ± 0·73	—	71·89 ± 1·30	56·17 ± 0·77	—	[illegible] ± 0·89
loured area	Both	—	—	73·96 ± 0·39	72·99	72·00 ± 0·42	54·46 ± 0·38	53·09	54·34 ± 0·59	—	58·07	—
ips)	♂	—	—	74·67 ± 0·49	—	71·95 ± 0·52	54·82	—	53·11 ± 0·81	—	—	—
	♀	—	—	72·95 ± 0·60	—	72·09 ± 0·68	54·06	—	55·62 ± 0·83	—	—	—
d	Both	25·40 ± 0·30	26·00	9·55 ± 0·11	9·74	10·67 ± 0·12	14·44 ± 0·11	14·49	14·76 ± 0·13	18·85 ± 0·18	13·12	[illegible] ± 0·30
	♂	26·05 ± 0·45	—	9·62 ± 0·14	—	10·59 ± 0·15	14·38 ± 0·15	—	15·00 ± 0·19	19·07 ± 0·22	—	[illegible] ± 0·42
	♀	24·90 ± 0·39	—	9·44 ± 0·16	—	10·80 ± 0·18	14·51 ± 0·17	—	14·67 ± 0·19	18·67 ± 0·28	—	[illegible] ± 0·38
	Both	1·82 ± 0·02	1·77	—	—	—	4·79 ± 0·05	—	4·88 ± 0·10	2·98 ± 0·05	—	3·16 ± 0·05
	Both	—	—	7·86 ± 0·11	7·69	6·89 ± 0·10	3·83 ± 0·05	3·73	3·82 ± 0·07	—	—	—
$\frac{-V}{R}$	Both	27·66 ± 0·41	25·89	35·18 ± 0·39	34·51	31·03 ± 0·46	34·38 ± 0·35	33·84	32·42 ± 0·40	34·09 ± 0·43	36·14	[illegible] ± 0·39

* Weighted by number of offspring.

and hybrids.

Selected parents of F_3* Pale	Medium	Dark	F_3 All 82 (48♂, 34♀)	Pale 29	Medium 31	Dark 22	*Polionotus-albifrons* cross F_1 95 (57♂, 38♀)	Back-cross 3/4 *polionotus* 76 (38♂, 38♀)	3/4 *albifrons* 51 (21♂, 30♀)
—	—	—	78·86±0·23	—	—	—	79·18±0·19	79·76±0·24	80·10±0·30
—	—	—	81·49±0·32	—	—	—	82·64±0·28	81·00±0·26	80·97±0·27
—	—	—	53·10±0·19	53·83	52·62	52·80	53·44±0·16	52·89±0·21	53·96±0·22
—	—	—	53·02±0·24	—	—	—	52·74±0·20	52·74±0·32	53·24±0·30
—	—	—	53·21±0·29	—	—	—	54·53±0·22	53·04±0·27	54·47±0·31
—	—	—	53·52	—	—	—	53·10	52·85	53·20
—	—	—	52·50	—	—	—	53·28	52·57	54·01
—	—	—	18·31±0·05	18·56	18·13	18·14	18·14±0·04	17·89±0·05	18·06±0·07
—	—	—	18·11±0·08	18·77	17·79	18·06	18·10±0·05	17·79±0·05	18·10±0·05
—	—	—	18·41	18·65	18·17	18·30	18·21	17·91	18·05
—	—	—	18·01	18·55	17·71	18·02	17·91	17·72	18·03
—	—	—	14·67±0·03	14·81	14·55	14·65	15·10±0·03	15·20±0·03	14·98±0·05
—	—	—	14·69±0·04	—	—	—	15·02±0·05	15·18±0·05	14·99±0·08
—	—	—	14·64±0·05	—	—	—	15·20±0·05	15·21±0·05	14·97±0·06
—	—	—	14·77	—	—	—	15·08	15·20	14·98
—	—	—	14·56	—	—	—	15·07	15·16	14·93
—	—	—	13·15±0·19	—	—	—	12·22±0·14	12·72±0·12	13·57±0·21
—	—	—	13·06±0·21	—	—	—	12·96±0·15	12·42±0·20	12·48±0·16
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
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—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
0·60	17·45	100·00	35·05	1·62	25·72	92·68	63·95	85·45	44·04
—	—	—	0·64±0·05	—	—	—	1·44±0·05	1·75±0·05	0·98±0·07
48·57	68·69	90·07	68·00±1·29	49·14	70·45	89·41	—	—	—
—	—	—	68·21±1·77	—	—	—	—	—	—
—	—	—	67·71±1·84	—	—	—	—	—	—
36·71	55·37	67·82	53·26±0·95	38·62	56·77	67·59	62·61±0·39	66·23±0·43	59·32±0·64
—	—	—	53·15±1·30	—	—	—	62·82±0·50	64·72±0·56	58·65±0·99
—	—	—	53·41±1·35	—	—	—	62·29±0·64	67·77±0·60	59·77±0·84
17·55	13·93	11·98	15·46±0·24	18·95	14·50	12·22	13·65±0·11	11·59±0·12	15·27±0·15
—	—	—	15·56±0·30	—	—	—	13·60±0·14	11·83±0·16	15·42±0·21
—	—	—	15·33±0·39	—	—	—	13·72±0·18	11·34±0·16	15·16±0·21
2·80	5·01	7·56	4·79±0·15	—	—	—	—	—	—
—	—	—	—	—	—	—	4·68±0·06	5·85±0·09	3·94±0·07
36·03	29·60	30·41	34·34±0·48	39·24	31·71	31·59	35·30±0·34	34·73±0·40	39·40±0·48

† "Corrected" means are the "actual" ones, reduced to a standard body length of 80 mm.

		Leucocephalus		*Albifrons*		F_1 (East Pass derivatives only)	F_2 (East Pass derivatives only)	Back-cross 3/4 *Leucocephalus*	Grades 7/8 *Leucocephalus*	F_3
	Sex	Wild	C_1	East Pass	C_1 generation (combined)					
Number ...		72 (33 ♂, 39 ♀)	46 (27 ♂, 19 ♀)	41 (25 ♂, 16 ♀)	50 (30 ♂, 20 ♀)	59 (31 ♂, 28 ♀)	75 (35 ♂, 40 ♀)	58 (35 ♂, 23 ♀)	41 (19 ♂, 22 ♀)	65 (41 ♂, 24 ♀)
Body length	♂	2·08 ±0·17	2·00 ±0·18	2·01 ±0·19	1·71 ±0·15	1·75 ±0·15	2·14 ±0·17	1·65 ±0·13	2·09 ±0·23	1·51 ±0·11
	♀	3·37 ±0·26	2·90 ±0·32	2·80 ±0·33	2·93 ±0·31	2·69 ±0·24	2·44 ±0·18	1·97 ±0·20	1·25 ±0·13	1·52 ±0·15
Tail length (actual)	Both	2·49 ±0·14	2·54 ±0·18	3·20 ±0·24	2·85 ±0·19	2·73 ±0·17	2·68 ±0·15	2·44 ±0·15	1·54 ±0·11	1·81 ±0·11
	♂	2·08 ±0·17	1·68 ±0·15	3·02 ±0·29	2·48 ±0·22	2·53 ±0·22	2·24 ±0·18	2·33 ±0·19	1·67 ±0·18	1·73 ±0·13
	♀	2·53 ±0·19	2·60 ±0·28	2·82 ±0·34	3·08 ±0·33	2·50 ±0·23	2·96 ±0·22	2·44 ±0·24	1·23 ±0·13	1·80 ±0·18
(corrected)*	♂	1·91	1·54	2·78	2·28	2·33	2·06	2·14	1·54	1·59
	♀	2·20	2·26	2·45	2·67	2·17	2·57	2·12	1·07	1·57
Foot length (actual)	♂	0·36 ±0·03	0·42 ±0·04	0·38 ±0·04	0·41 ±0·04	0·41 ±0·04	0·40 ±0·03	0·40 ±0·03	0·32 ±0·03	0·41 ±0·03
	♀	0·47 ±0·04	0·24 ±0·03	0·41 ±0·05	0·46 ±0·05	0·68 ±0·06	0·43 ±0·03	0·40 ±0·04	0·33 ±0·03	0·30 ±0·03
(corrected)	♂	0·33	0·38	0·35	0·38	0·38	0·37	0·37	0·30	0·38
	♀	0·43	0·22	0·38	0·42	0·62	0·39	0·37	0·30	0·28
Ear length (actual)	Both	0·48 ±0·03	0·44 ±0·03	0·54 ±0·04	0·64 ±0·04	0·46 ±0·03	0·41 ±0·02	0·38 ±0·02	0·42 ±0·03	0·47 ±0·03
	♂	0·41 ±0·03	0·47 ±0·04	0·53 ±0·05	0·57 ±0·05	0·47 ±0·04	0·43 ±0·03	0·39 ±0·03	0·35 ±0·04	0·45 ±0·03
	♀	0·45 ±0·03	0·40 ±0·04	0·50 ±0·06	0·64 ±0·07	0·45 ±0·04	0·39 ±0·03	0·34 ±0·03	0·48 ±0·05	0·51 ±0·05
(corrected)	♂	0·39	0·45	0·51	0·55	0·45	0·41	0·38	0·33	0·43
	♀	0·43	0·39	0·48	0·61	0·43	0·38	0·32	0·46	0·49
Weight	♂	1·45 ±0·12	1·57 ±0·14	1·41 ±0·13	1·55 ±0·13	1·10 ±0·09	1·35 ±0·11	1·48 ±0·12	1·51 ±0·17	1·69 ±0·13
	♀	1·58 ±0·12	1·71 ±0·19	1·00 ±0·12	1·69 ±0·18	1·56 ±0·14	1·54 ±0·12	1·10 ±0·11	1·32 ±0·13	1·25 ±0·12
Caudal vertebrae	Both	0·64 ±0·04	—	0·90 ±0·07	—	0·72 ±0·04	0·84 ±0·05	—	—	—
Right pelvis (actual)	♂	0·40 ±0·03	—	0·39 ±0·04	—	0·42 ±0·04	0·43 ±0·03	—	—	—
	♀	0·67 ±0·05	—	0·53 ±0·06	—	0·61 ±0·06	0·53 ±0·04	—	—	—
(corrected)	♂	0·31	—	0·30	—	0·32	0·33	—	—	—
	♀	0·40	—	0·32	—	0·37	0·32	—	—	—
Right femur (actual)	♂	0·36 ±0·03	—	0·36 ±0·03	—	0·31 ±0·03	0·45 ±0·04	—	—	—
	♀	0·51 ±0·04	—	0·56 ±0·07	—	0·53 ±0·05	0·56 ±0·04	—	—	—
(corrected)	♂	0·28	—	0·28	—	0·24	0·35	—	—	—
	♀	0·31	—	0·34	—	0·32	0·34	—	—	—
Skull length (actual)	♂	0·40 ±0·03	—	0·41 ±0·04	—	0·52 ±0·04	0·48 ±0·04	—	—	—
	♀	0·46 ±0·04	—	0·45 ±0·05	—	0·57 ±0·05	0·51 ±0·04	—	—	—
(corrected)	♂	0·28	—	0·29	—	0·37	0·34	—	—	—
	♀	0·35	—	0·34	—	0·43	0·39	—	—	—
Skull breadth (actual)	♂	0·19 ±0·02	—	0·21 ±0·02	—	0·18 ±0·02	0·21 ±0·02	—	—	—
	♀	0·18 ±0·01	—	0·14 ±0·02	—	0·17 ±0·02	0·18 ±0·01	—	—	—
Tail stripe	Both	—	—	30·13	36·08	5·65	16·22	4·33	—	31·79
Foot pigment	Both	—	—	—	—	—	—	—	—	—
Coloured area (base)	Both	3·81 ±0·23	3·44 ±0·25	3·05 ±0·23	5·96 ±0·41	3·04 ±0·18	5·75 ±0·32	4·65 ±0·29	4·27 ±0·32	7·29 ±0·43
	♂	3·59 ±0·32	3·13 ±0·30	3·02 ±0·30	6·60 ±0·58	3·27 ±0·27	4·88 ±0·39	5·17 ±0·42	3·66 ±0·40	7·36 ±0·55
	♀	3·94 ±0·31	3·51 ±0·37	3·14 ±0·37	4·74 ±0·53	2·74 ±0·24	6·43 ±0·49	3·71 ±0·37	4·72 ±0·48	7·19 ±0·70
Coloured area (tips)	Both	—	—	5·00 ±0·38	—	—	—	—	—	—
	♂	—	—	5·07 ±0·50	—	—	—	—	—	—
	♀	—	—	4·87 ±0·58	—	—	—	—	—	—
Red	Both	3·53 ±0·21	4·18 ±0·30	1·37 ±0·10	1·31 ±0·09	1·50 ±0·09	2·61 ±0·14	2·99 ±0·19	3·14 ±0·23	3·29 ±0·19
	♂	3·50 ±0·32	4·18 ±0·41	1·20 ±0·12	1·42 ±0·13	1·55 ±0·13	2·29 ±0·18	2·96 ±0·24	2·94 ±0·32	3·49 ±0·26
	♀	3·46 ±0·28	4·13 ±0·43	1·54 ±0·18	1·08 ±0·12	1·19 ±0·11	2·84 ±0·22	2·99 ±0·30	3·28 ±0·33	2·69 ±0·26
$\frac{A_b}{R}$	Both	0·29 ±0·02	0·30 ±0·02	0·31 ±0·02	0·48 ±0·03	0·31 ±0·02	0·55 ±0·03	0·43 ±0·03	0·29 ±0·02	0·70 ±0·04
$\frac{R-Y}{R}$	Both	4·82 ±0·29	4·93 ±0·35	5·09 ±0·38	5·73 ±0·40	4·33 ±0·26	6·02 ±0·33	4·48 ±0·28	5·07 ±0·38	6·54 ±0·39

* Standard deviations for certain body parts have been "corrected" by the elimination of that part of the total variation which is due to variation in general body size. This is effected by multiplying the gross standard deviation by $\sqrt{1-r^2}$, r being the coefficient of correlation between body length and the character in question.

Correlation

	Sex	*Leucocephalus* Wild Gross	*Leucocephalus* Wild Net*	*Leucocephalus* C_1 Gross	*Leucocephalus* C_1 Net	*Albifrons* East Pass Gross	*Albifrons* East Pass Net	*Polionotus* Wild Gross	*Polionotus* Wild Net	*Polionotus* C_1 Gross	*Polionotus* C_1 Net	*Leuc.-alb.* F_1 Gross	*Leuc.-alb.* F_1 Net	*Leuc.-alb.* F_2 Gross	*Leuc.-alb.* F_2 Net	(
Tail—Foot	♂	+·455 ±·093	+·356	+·388 ±·110	+·278	+·388 ±·115	+·279	+·765 ±·054	+·721	+·292 ±·099	+·165	+·731 ±·056	+·681	+·533 ±·082	+·448	+
	♀	+·597 ±·070	+·502	+·384 ±·132	+·236	+·813 ±·057	+·772	+·780 ±·061	+·731	+·604 ±·094	+·511	+·551 ±·089	+·445	+·251 ±·100	+·070	+
Tail—Ear	Both	+·404 ±·066	+·314	+·364 ±·086	+·265	+·400 ±·089	+·309	+·442 ±·080	+·360	+·329 ±·080	+·222	+·165 ±·085	+·022	+·151 ±·076	+·005	+
Tail—Tail stripe	Both	—	—	—	—	−·225 ±·100	—	—	—	—	—	−·009 ±·088	—	−·052 ±·078	—	-
Tail—Foot pigm.	Both	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Tail—Coloured area, base	Both	+·239 ±·075	—	+·081 ±·099	—	−·317 ±·095	—	—	—	—	—	+·095 ±·087	—	−·098 ±·077	—	-
Tail—Coloured area, tips	Both	—	—	—	—	—	—	−·260 ±·093	—	−·052 ±·087	—	—	—	—	—	
Tail—Red	Both	−·014 ±·079	—	−·085 ±·099	—	+·203 ±·101	—	+·134 ±·098	—	+·190 ±·084	—	−·180 ±·085	—	−·059 ±·078	—	
Foot—Ear	♂	+·131 ±·116	+·020	+·277 ±·120	+·186	+·213 ±·129	+·113	+·450 ±·103	+·383	+·336 ±·096	+·253	+·179 ±·117	+·074	+·394 ±·096	+·319	
	♀	+·405 ±·090	+·332	+·111 ±·153	−·002	+·556 ±·117	+·503	+·456 ±·123	+·390	+·357 ±·131	+·278	+·524 ±·092	+·467	+·105 ±·106	−·009	
Foot—Tail stripe	♂	—	—	—	—	−·291 ±·123	—	—	—	—	—	−·145 ±·119	—	−·209 ±·109	—	
	♀	—	—	—	—	+·039 ±·168	—	—	—	—	—	+·176 ±·124	—	−·252 ±·100	—	
Foot—Coloured area, base	♂	−·023 ±·118	—	+·043 ±·129	—	−·131 ±·133	—	—	—	—	—	+·064 ±·121	—	−·315 ±·103	—	
	♀	+·290 ±·099	—	−·377 ±·133	—	−·140 ±·165	—	—	—	—	—	+·286 ±·119	—	−·180 ±·103	—	
Foot—Coloured area, tips	♂	—	—	—	—	—	—	−·167 ±·126	—	+·040 ±·108	—	—	—	—	—	
	♀	—	—	—	—	—	—	−·120 ±·153	—	+·265 ±·137	—	—	—	—	—	
Foot—Red	♂	+·175 ±·114	—	−·042 ±·129	—	+·441 ±·109	—	+·240 ±·122	—	+·149 ±·106	—	+·037 ±·121	—	+·223 ±·108	—	
	♀	−·245 ±·102	—	−·336 ±·137	—	−·110 ±·166	—	+·366 ±·134	—	−·007 ±·147	—	+·007 ±·128	—	+·076 ±·106	—	
Foot—Foot pigment	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	♀	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Tail stripe—Foot pigm.	Both	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Tail stripe—Coloured area, base	Both	—	—	—	—	+·464 ±·083	—	—	—	—	—	+·649 ±·051	—	+·598 ±·050	—	
Tail stripe—Coloured area, tips	Both	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Tail stripe—Red	Both	—	—	—	—	−·586 ±·069	—	—	—	—	—	−·190 ±·085	—	−·455 ±·062	—	
Foot pigm.—Coloured area, base	Both	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Foot pigm.—Coloured area, tips	Both	—	—	—	—	—	—	+·168 ±·097	—	—	—	—	—	—	—	
Foot pigm.—Red	Both	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Coloured area, base—Red	Both	−·310 ±·072	—	−·191 ±·096	—	−·373 ±·091	—	—	—	—	—	−·326 ±·077	—	−·682 ±·042	—	
Coloured area, tips—Red	Both	—	—	—	—	−·446 ±·084	—	−·426 ±·081	—	−·615 ±·054	—	—	—	—	—	
Coloured area, base—$\frac{R-V}{R}$	Both	+·418 ±·069	—	+·119 ±·098	—	−·220 ±·100	—	—	—	—	—	−·000	—	−·299 ±·071	—	
Coloured area, tips—$\frac{R-V}{R}$	Both	—	—	—	—	—	—	−·158 ±·097	—	−·647 ±·051	—	—	—	—	—	
Coloured area, base-tips	Both	—	—	—	—	+·637 ±·063	—	—	—	—	—	+·778 ±·051	—	—	—	
Red—$\frac{R-V}{R}$	Both	−·309 ±·076	—	−·310 ±·090	—	+·546 ±·074	—	+·250 ±·094	—	+·803 ±·031	—	+·455 ±·070	—	+·436 ±·063	—	

* "Net" correlations are those from which the influence of ge

TABLE V.

s between various characters.

3/4 leuc.		*7/8 leuc.*		*Leuc.-alb. F_2*		*Leuc.-pol. F_1*		*Leuc.-pol. F_2*		*3/4 leuc.*		*7/8 leuc.*		*Leuc.-pol. F_3*		*Pol.-alb. F_1*		*3/4 pol.*		*3/4 alb.*	
Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net
·412 ±·093	+·307	+·120 ±·153	−·038	+·482 ±·081	+·388	+·512 ±·082	+·425	+·675 ±·049	+·615	+·116 ±·119	−·042	+·191 ±·110	+·046	+·433 ±·079	+·331	+·578 ±·059	+·501	+·749 ±·048	+·702	+·735 ±·068	+·686
·294 ±·128	+·124	+·027 ±·144	−·210	+·125 ±·135	−·087	+·679 ±·061	+·605	+·662 ±·052	+·584	+·354 ±·098	+·199	+·302 ±·137	+·134	+·548 ±·081	+·441	+·464 ±·087	+·338	+·654 ±·063	+·574	+·367 ±·106	+·215
·186 ±·086	+·048	+·512 ±·078	+·445	+·403 ±·070	+·312	+·473 ±·061	+·396	+·358 ±·056	+·257	+·365 ±·071	+·266	+·617 ±·056	+·573	+·380 ±·064	+·284	+·466 ±·055	+·388	+·276 ±·071	+·157	+·279 ±·087	+·161
−·130 ±·087	—	—	—	+·350 ±·073	—	+·033 ±·078	—	+·005 ±·065	—	+·165 ±·080	—	—	—	−·189 ±·072	—	+·008 ±·069	—	−·221 ±·074	—	−·224 ±·090	—
—	—	—	—	—	—	—	—	−·002 ±·065	—	+·043 ±·082	—	—	—	−·289 ±·068	—	+·025 ±·069	—	−·016 ±·077	—	−·277 ±·087	—
−·161 ±·086	—	−·008 ±·105	—	+·198 ±·080	—	—	—	+·001 ±·065	—	−·010 ±·082	—	−·392 ±·077	—	−·154 ±·073	—	—	—	—	—	—	—
—	—	—	—	—	—	+·120 ±·077	—	−·039 ±·064	—	—	—	—	—	−·261 ±·069	—	−·134 ±·068	—	−·082 ±·077	—	−·271 ±·088	—
+·112 ±·087	—	−·111 ±·104	—	−·269 ±·078	—	−·276 ±·072	—	−·109 ±·064	—	−·184 ±·080	—	+·281 ±·084	—	+·160 ±·073	—	+·103 ±·069	—	+·228 ±·073	—	+·017 ±·094	—
+·475 ±·089	+·411	+·068 ±·154	−·051	+·192 ±·101	+·090	+·478 ±·083	+·385	+·478 ±·070	+·415	+·273 ±·112	+·182	+·238 ±·107	+·142	+·327 ±·087	+·243	+·355 ±·078	+·275	+·473 ±·084	+·409	+·014 ±·147	−·112
+·335 ±·124	+·253	+·301 ±·131	+·214	−·272 ±·127	−·437	+·261 ±·106	+·168	+·399 ±·078	+·325	+·440 ±·090	+·372	+·120 ±·149	+·008	+·441 ±·093	+·373	+·463 ±·086	+·398	+·196 ±·105	+·094	+·452 ±·098	+·385
+·097 ±·113	—	—	—	−·099 ±·104	—	−·433 ±·088	—	−·258 ±·084	—	−·033 ±·121	—	—	—	−·243 ±·090	—	−·038 ±·089	—	−·120 ±·108	—	−·195 ±·142	—
+·227 ±·133	—	—	—	−·463 ±·108	—	−·180 ±·110	—	−·118 ±·091	—	−·330 ±·100	—	—	—	−·120 ±·114	—	+·425 ±·090	—	−·040 ±·109	—	−·453 ±·098	—
+·167 ±·111	—	−·162 ±·151	—	−·166 ±·102	—	−·044 ±·109	—	−·247 ±·089	—	+·081 ±·120	—	+·211 ±·109	—	−·355 ±·085	—	—	—	—	—	—	—
+·310 ±·127	—	−·339 ±·127	—	−·153 ±·134	—	+·154 ±·112	—	−·260 ±·086	—	−·188 ±·108	—	+·365 ±·131	—	−·374 ±·099	—	—	—	—	—	—	—
—	—	—	—	—	—	−·139 ±·107	—	−·223 ±·086	—	—	—	—	—	−·376 ±·084	—	−·049 ±·089	—	−·126 ±·108	—	−·169 ±·143	—
—	—	—	—	—	—	+·006 ±·114	—	−·329 ±·083	—	—	—	—	—	−·476 ±·089	—	+·333 ±·097	—	−·002 ±·109	—	−·382 ±·105	—
−·116 ±·113	—	−·196 ±·149	—	+·092 ±·105	—	−·084 ±·107	—	+·225 ±·086	—	−·075 ±·120	—	+·012 ±·114	—	+·387 ±·083	—	−·050 ±·089	—	+·248 ±·103	—	+·062 ±·147	—
+·140 ±·138	—	−·096 ±·143	—	+·253 ±·129	—	−·041 ±·114	—	+·068 ±·092	—	+·185 ±·108	—	−·063 ±·150	—	+·515 ±·085	—	−·381 ±·094	—	+·034 ±·109	—	+·184 ±·119	—
—	—	—	—	—	—	—	—	+·044 ±·090	—	—	—	—	—	−·307 ±·088	—	+·068 ±·089	—	−·300 ±·100	—	−·335 ±·131	—
—	—	—	—	—	—	—	—	−·069 ±·092	—	—	—	—	—	−·390 ±·098	—	−·003 ±·109	—	+·087 ±·109	—	−·292 ±·113	—
—	—	—	—	—	—	−·001 ±·078	—	+·133 ±·063	—	+·096 ±·082	—	—	—	+·157 ±·073	—	+·100 ±·068	—	+·140 ±·076	—	+·372 ±·081	—
+·538 ±·063	—	—	—	+·758 ±·036	—	+·467 ±·061	—	+·784 ±·025	—	+·637 ±·049	—	—	—	+·898 ±·014	—	—	—	—	—	—	—
—	—	—	—	—	—	+·706 ±·039	—	+·755 ±·028	—	—	—	—	—	+·840 ±·022	—	+·674 ±·038	—	+·660 ±·044	—	+·763 ±·040	—
−·245 ±·083	—	—	—	−·536 ±·060	—	−·133 ±·077	—	−·597 ±·042	—	−·414 ±·068	—	—	—	−·701 ±·038	—	−·420 ±·057	—	−·605 ±·051	—	−·338 ±·084	—
—	—	—	—	—	—	—	—	—	—	+·154 ±·080	—	—	—	+·209 ±·071	—	—	—	—	—	—	—
—	—	—	—	—	—	−·158 ±·076	—	+·165 ±·063	—	—	—	—	—	+·207 ±·071	—	+·123 ±·068	—	+·305 ±·070	—	+·461 ±·074	—
—	—	—	—	—	—	−·171 ±·076	—	−·192 ±·062	—	−·165 ±·080	—	—	—	−·318 ±·067	—	−·123 ±·068	—	−·310 ±·070	—	−·157 ±·092	—
−·547 ±·062	—	−·117 ±·104	—	−·788 ±·032	—	+·017 ±·078	—	−·627 ±·039	—	−·688 ±·043	—	−·711 ±·045	—	−·823 ±·024	—	—	—	—	—	—	—
—	—	—	—	—	—	−·330 ±·070	—	−·600 ±·041	—	—	—	—	—	−·858 ±·020	—	−·526 ±·050	—	−·744 ±·034	—	−·472 ±·073	—
+·156 ±·086	—	−·042 ±·105	—	−·538 ±·059	—	—	—	—	—	−·182 ±·080	—	—	—	−·451 ±·059	—	—	—	—	—	—	—
—	—	—	—	—	—	−·096 ±·078	—	−·350 ±·057	—	—	—	—	—	−·545 ±·052	—	−·203 ±·066	—	−·393 ±·065	—	−·199 ±·091	—
—	—	—	—	—	—	+·458 ±·062	—	+·891 ±·012	—	—	—	—	—	+·951 ±·071	—	—	—	—	—	—	—
−·039 ±·088	—	−·210 ±·101	—	+·729 ±·039	—	+·700 ±·040	—	+·529 ±·047	—	+·364 ±·071	—	−·177 ±·088	—	+·633 ±·045	—	+·669 ±·038	—	+·624 ±·047	—	+·701 ±·048	—

neral body size has been eliminated by the use of the method of partial correlation.

TABLE IV.

Standard deviations.

Number ...	Sex	*Leucocephalus and polionotus and hybrids*: *Leucocephalus* Wild 72 (33 ♂, 39 ♀)	*Polionotus* Wild 46 (27 ♂, 19 ♀)	*Polionotus* C_1 60 (39 ♂, 21 ♀)	F_1 74 (39 ♂, 35 ♀)	F_2 109 (56 ♂, 53 ♀)	3/4 *Leucocephalus* 67 (31 ♂, 36 ♀)	7/8 *Leucocephalus* 55 (35 ♂, 20 ♀)	F_3 82 (48 ♂, 34 ♀)	*Polionotus-albifrons* hybrids: F_1 95 (57 ♂, 38 ♀)	3/4 *Polionotus* 76 (38 ♂, 38 ♀)	3/4 *Albifrons* 51 (21 ♂, 30 ♀)
Body length	♂	2·08 ±0·17	1·77 ±0·16	2·04 ±0·16	1·75 ±0·13	2·33 ±0·15	2·32 ±0·20	1·79 ±0·14	2·39 ±0·16	2·11 ±0·13	2·20 ±0·17	2·06 ±0·21
	♀	3·37 ±0·26	3·77 ±0·41	2·96 ±0·31	3·07 ±0·25	2·89 ±0·19	2·99 ±0·24	2·26 ±0·24	2·73 ±0·22	2·60 ±0·20	2·42 ±0·19	2·22 ±0·19
Tail length	Both	2·49 ±0·14	3·19 ±0·22	2·70 ±0·17	2·98 ±0·17	2·82 ±0·13	2·14 ±0·12	2·31 ±0·15	2·49 ±0·13	2·31 ±0·11	2·73 ±0·15	2·38 ±0·16
(actual)	♂	2·08 ±0·17	2·42 ±0·22	2·23 ±0·17	2·34 ±0·18	2·44 ±0·16	1·95 ±0·17	2·23 ±0·18	2·51 ±0·17	2·20 ±0·14	2·94 ±0·23	2·03 ±0·21
	♀	2·53 ±0·19	3·16 ±0·35	2·67 ±0·28	2·85 ±0·23	2·99 ±0·20	2·24 ±0·18	2·43 ±0·26	2·47 ±0·20	2·05 ±0·16	2·50 ±0·19	2·48 ±0·22
(corrected)*	♂	1·91	2·23	2·05	2·15	2·24	1·79	2·05	2·31	2·02	2·70	1·87
	♀	2·20	2·75	2·32	2·48	2·60	1·95	2·11	2·15	1·78	2·17	2·16
Foot length	♂	0·36 ±0·03	0·48 ±0·04	0·38 ±0·03	0·44 ±0·03	0·59 ±0·04	0·38 ±0·03	0·39 ±0·03	0·48 ±0·03	0·47 ±0·03	0·49 ±0·04	0·46 ±0·05
(actual)	♀	0·47 ±0·04	0·54 ±0·06	0·51 ±0·05	0·61 ±0·05	0·55 ±0·04	0·40 ±0·03	0·41 ±0·04	0·70 ±0·06	0·45 ±0·03	0·45 ±0·03	0·44 ±0·04
(corrected)	♂	0·33	0·44	0·35	0·41	0·54	0·35	0·36	0·44	0·43	0·45	0·42
	♀	0·43	0·50	0·47	0·56	0·51	0·37	0·38	0·64	0·42	0·41	0·40
Ear length	Both	0·48 ±0·03	0·68 ±0·05	0·48 ±0·03	0·47 ±0·03	0·54 ±0·02	0·37 ±0·02	0·36 ±0·02	0·44 ±0·02	0·49 ±0·02	0·46 ±0·02	0·50 ±0·03
(actual)	♂	0·41 ±0·03	0·68 ±0·06	0·47 ±0·04	0·45 ±0·03	0·56 ±0·04	0·33 ±0·03	0·39 ±0·03	0·45 ±0·03	0·52 ±0·03	0·47 ±0·04	0·54 ±0·06
	♀	0·45 ±0·03	0·67 ±0·07	0·47 ±0·05	0·48 ±0·04	0·52 ±0·03	0·38 ±0·03	0·29 ±0·03	0·41 ±0·03	0·44 ±0·03	0·44 ±0·03	0·48 ±0·04
(corrected)	♂	0·39	0·65	0·45	0·44	0·53	0·32	0·38	0·43	0·50	0·45	0·51
	♀	0·43	0·64	0·45	0·46	0·50	0·37	0·28	0·40	0·42	0·42	0·46
Weight	♂	1·45 ±0·12	1·42 ±0·13	1·87 ±0·14	1·62 ±0·12	1·74 ±0·11	1·75 ±0·15	1·31 ±0·11	1·97 ±0·14	1·62 ±0·10	1·14 ±0·09	1·46 ±0·15
	♀	1·58 ±0·12	2·12 ±0·23	2·93 ±0·30	2·23 ±0·18	1·77 ±0·12	1·80 ±0·14	1·68 ±0·18	1·82 ±0·15	1·38 ±0·11	1·80 ±0·14	1·28 ±0·11
Caudal vertebrae	Both	0·64 ±0·04	0·80 ±0·06	—	0·66 ±0·04	0·83 ±0·04	—	—	—	—	—	—
Right pelvis	♂	0·40 ±0·03	0·52 ±0·05	—	0·38 ±0·03	0·51 ±0·03	—	—	—	—	—	—
(actual)	♀	0·67 ±0·05	0·61 ±0·07	—	0·73 ±0·06	0·67 ±0·04	—	—	—	—	—	—
(corrected)	♂	0·31	0·40	—	0·29	0·39	—	—	—	—	—	—
	♀	0·40	0·37	—	0·44	0·40	—	—	—	—	—	—
Right femur	♂	0·36 ±0·03	0·55 ±0·05	—	0·36 ±0·03	0·47 ±0·03	—	—	—	—	—	—
(actual)	♀	0·51 ±0·04	0·77 ±0·08	—	0·92 ±0·07	0·58 ±0·04	—	—	—	—	—	—
(corrected)	♂	0·28	0·42	—	0·28	0·36	—	—	—	—	—	—
	♀	0·31	0·46	—	0·55	0·35	—	—	—	—	—	—
Skull length	♂	0·40 ±0·03	0·43 ±0·04	—	0·44 ±0·03	0·51 ±0·03	—	—	—	—	—	—
(actual)	♀	0·46 ±0·04	0·62 ±0·07	—	0·60 ±0·05	0·77 ±0·05	—	—	—	—	—	—
(corrected)	♂	0·28	0·30	—	0·31	0·36	—	—	—	—	—	—
	♀	0·35	0·47	—	0·46	0·58	—	—	—	—	—	—
Skull breadth	♂	0·19 ±0·02	0·22 ±0·02	—	0·15 ±0·01	0·22 ±0·01	—	—	—	—	—	—
(actual)	♀	0·18 ±0·01	0·32 ±0·04	—	0·20 ±0·02	0·23 ±0·02	—	—	—	—	—	—
Tail stripe	Both	—	—	—	24·70	33·72	3·23	2·94	42·42	34·18	24·96	35·31
Foot pigment	Both	—	0·83 ±0·06	0·80 ±0·05	0·85 ±0·05	0·81 ±0·04	0·61 ±0·04	—	0·67 ±0·04	0·69 ±0·03	0·63 ±0·03	0·73 ±0·05
Coloured area	Both	3·81 ±0·23	—	—	6·46 ±0·35	13·87 ±0·64	6·05 ±0·36	6·37 ±0·41	17·27 ±0·91	—	—	—
(base)	♂	3·59 ±0·32	—	—	6·37 ±0·48	13·16 ±0·85	4·85 ±0·42	6·55 ±0·53	18·17 ±1·25	—	—	—
	♀	3·94 ±0·31	—	—	6·47 ±0·51	14·05 ±0·92	6·75 ±0·54	5·87 ±0·63	15·91 ±1·30	—	—	—
Coloured area	Both	—	3·91 ±0·27	4·81 ±0·29	4·89 ±0·27	9·02 ±0·41	—	—	12·70 ±0·67	5·54 ±0·28	5·36 ±0·30	6·74 ±0·45
(tips)	♂	—	3·75 ±0·34	4·85 ±0·37	4·72	8·87 ±0·57	—	—	13·36 ±0·92	5·48 ±0·35	5·03 ±0·40	6·56 ±0·70
	♀	—	3·91 ±0·43	4·73 ±0·48	5·05	9·00 ±0·59	—	—	11·70 ±0·96	5·63 ±0·45	5·24 ±0·42	6·81 ±0·59
Red	Both	3·53 ±0·21	1·06 ±0·08	1·34 ±0·08	1·43 ±0·08	2·05 ±0·09	2·17 ±0·13	3·32 ±0·21	3·17 ±0·17	1·59 ±0·08	1·45 ±0·08	1·58 ±0·11
	♂	3·50 ±0·32	1·07 ±0·10	1·37 ±0·10	1·36 ±0·10	2·09 ±0·14	1·82 ±0·16	3·67 ±0·30	3·04 ±0·21	1·58 ±0·10	1·48 ±0·12	1·37 ±0·15
	♀	3·46 ±0·28	1·02 ±0·11	1·28 ±0·13	1·51 ±0·12	2·02 ±0·13	2·44 ±0·20	2·55 ±0·27	3·36 ±0·27	1·60 ±0·13	1·38 ±0·11	1·70 ±0·15
$\frac{A_b}{R}$	Both	0·29 ±0·02	—	—	0·65 ±0·04	1·53 ±0·07	0·62 ±0·04	0·52 ±0·03	2·01 ±0·11	—	—	—
$\frac{A_t}{R}$	Both	—	1·13 ±0·08	1·16 ±0·07	0·60 ±0·03	1·08 ±0·05	—	—	—	0·80 ±0·04	1·13 ±0·06	0·72 ±0·05
$\frac{R-V}{R}$	Both	4·82 ±0·29	3·88 ±0·28	5·33 ±0·33	4·49 ±0·25	6·05 ±0·28	5·18 ±0·31	4·26 ±0·27	6·45 ±0·34	4·84 ±0·24	5·05 ±0·29	5·05 ±0·34

TABLE VI.

Parent-offspring correlations.

Generations	No. of parents	No. of off-spring	Foot length	Foot pigmen-tation	A_b	A_t	Red	$\frac{A}{R}$	$\frac{R-V}{R}$
Leucocephalus, P–C_1	21	46	−0·036	—	+0·303	—	+0·486	+0·500	+0·075
Albifrons, P–C_1	25	49	+0·258	—	+0·668	—	+0·201	+0·556	+0·431
Polionotus, P–C_1	21	61	+0·368	+0·195	—	+0·387	+0·463	—	—
Leucocephalus–leucocephalus-albifrons, F_1 ...	19	72	—	—	+0·317	—	+0·296	+0·458	−0·045
Albifrons–leucocephalus-albifrons, F_1	15	73	—	—	+0·560	—	+0·016	+0·277	+0·135
Leucocephalus-albifrons, F_1–F_2	30	122	+0·041	—	+0·510	—	+0·276	+0·291	+0·046
Leucocephalus–leucocephalus-albifrons, back-cross	11	67	—	—	+0·289	—	+0·224	+0·224	−0·060
F_1–*leucocephalus-albifrons* back-cross	18	70	—	—	+0·237	—	+0·200	+0·075	+0·091
Leucocephalus–grades	4	37	—	—	+0·318	—	+0·359	+0·211	−0·283
Back-cross–grades	14	58	—	—	−0·390	—	+0·366	+0·101	+0·308
Leucocephalus-albifrons, F_2–F_3	22	65	+0·114	—	+0·751	—	+0·743	+0·762	+0·381
Leucocephalus–leucocephalus-polionotus, F_1 ...	17	72	—	—	+0·458	—	−0·099	—	—
Polionotus–leucocephalus-polionotus, F_1	12	66	—	+0·576	—	+0·237	+0·233	—	—
Leucocephalus-polionotus, F_1–F_2	37	108	+0·110	+0·362	+0·219	+0·417	+0·092	—	—
Leucocephalus–leucocephalus-polionotus back-cross	13	65	—	—	−0·207	—	+0·094	—	—
F_1–*leucocephalus-polionotus* back-cross	13	66	—	+0·076	+0·122	—	+0·253	—	—
Leucocephalus–grades	10	42	—	—	+0·300	—	+0·481	—	—
Back-cross–grades	10	55	—	—	+0·616	—	+0·343	—	—
Leucocephalus-polionotus, F_2–F_3	26	82	+0·298	+0·250	—	+0·917	+0·837	—	—
Polionotus–polionotus-albifrons, F_1	13	85	—	+0·271	—	+0·402	—	—	—
Albifrons–polionotus-albifrons, F_1	6	49	—	—	—	+0·601	—	—	—
Polionotus–back-cross (3/4 *polionotus*)	12	73	—	−0·378	—	+0·249	—	—	—
F_1–back-cross (3/4 *polionotus*)	14	69	—	+0·184	—	+0·216	—	—	—
Albifrons–back-cross (3/4 *albifrons*)	4	25	—	—	—	+0·521	—	—	—
F_1–back-cross (3/4 *albifrons*)	11	48	—	+0·473	—	+0·734	—	—	—

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THE GENETICS OF *GEUM INTERMEDIUM* WILLD. HAUD EHRH.[1], AND ITS BACK-CROSSES.

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(With Plates XII–XV and One Map.)

INTRODUCTION.

Geum urbanum and *G. rivale* are widely distributed in Britain, the former occurring in 108 vice-counties[2], the later in 101, and *G. intermedium*, the result of the cross between the two species, is recorded from 70[3]. *G. urbanum* is found in hedge-banks and on borders of woods, while *G. rivale* and *G. intermedium* grow in damp woods, copses and meadows.

The first recorded experiments under control with these species would seem to have been made by Gartner[4] in 1849. Sowerby[5] gives a description and figure of *G. intermedium* and says "that it is quite intermediate in appearance between *G. urbanum* and *G. rivale*, between which it may be a hybrid." The late Dr Bell Slater[6] produced a hybrid *Geum* by crossing *G. rivale* with *G. urbanum*. He says, "the result obtained was a set of plants intermediate in characters between the parent forms, and perfectly identical with the wild plant, the *Geum intermedium* of Ehrhart, such as I have myself found growing in Scotland, when botanising, some years since, in the neighbourhood of Edinburgh." It is of considerable interest that Bell Slater obtained a generation by crossing in this way. For two years in succession I tried to make the hybrid with *G. rivale* as the seed parent, making many crosses each year, but failed to obtain a single viable seed, indeed frequently the achenes never developed at all.

The figure of *G. intermedium* given by Sowerby[7] is not typical of the F_1 plant obtained by crossing the two species, the flowers being much

[1] *Journ. Bot.* 1930, LXVIII, 88.

[2] Cf. H. C. Watson, *Topographical Botany*, 2nd edit., 1883.

[3] *London Catalogue of British Plants*, 1925, ed. XI, 17.

[4] *Über die Bastarderzeugung im Pflanzenreich*, Stuttgart, 1849. (*The Production of Hybrids in the Plant Kingdom.*)

[5] Sowerby's *English Botany*, 1873, III, 199.

[6] *Phyt.* 1852, Ser. 1, IV, 739.

[7] Sowerby's *English Botany*, 1873, III, Fig. ccclviii.

too open, but it agrees closely with plants obtained by crossing *G. intermedium* with *G. urbanum*. Bentham and Hooker[1] state that "where *G. rivale* and *G. urbanum* grow together, specimens are occasionally found approaching sometimes more nearly to the one, sometimes to the other. They have been described as a species under the name of *G. intermedium* Ehrh., but they are more generally believed to be mere accidental hybrids between the two species." The first part of this statement describes exactly what is found where the species overlap, plants approaching one or the other of the species with a very definite "accidental" hybrid, *G. intermedium*, growing amongst them. Those plants that approach *G. urbanum* are the result of back-crosses between *G. intermedium* and *G. urbanum* or *vice versa*, those approaching *G. rivale* and almost indistinguishable from it have resulted from a back-cross between *G. intermedium* and *G. rivale* or the reciprocal, while yet others have been derived from the F_1 generation of *G. intermedium*.

In 1912 Weiss[2] read before the British Association his paper on *G. intermedium* Ehrh. and its segregates. He demonstrated clearly that the hybrid, on selfing, does not breed true, but that considerable segregation takes place. In 1916 Rosen[3] published a paper on Hybridisation Experiments with *Geum urbanum* × *rivale*, giving very full details of his researches. Since the publication of these papers Blaringham[4] has averred that *G. intermedium* breeds true, but his own descriptions show that this is an erroneous conclusion drawn from the results he himself obtained. In my own researches with the hybrid, which in some of the characters investigated overlap with those of Weiss and Rosen, but include others which they do not mention, segregation does take place; my evidence, if it is needed, proves very clearly that these authors are right. It is quite inconceivable to me how Blaringham could possibly have arrived at any other conclusion, the fact that segregation takes place being quite obvious from a cursory examination of a batch of F_2 seedlings without any critical analysis.

Origin of plants used in experiments at Potterne, 1924–8.

Four plants were collected in the wild as follows:

G. urbanum, Stock plant A. Potterne, Wiltshire.

G. rivale, Stock plant C. Nith Valley, Dumfriesshire.

[1] *The British Flora*, 1918, p. 132.

[2] *British Association*, 1912, p. 675.

[3] *Botaniska Notiser för år* 1916, pp. 163–72.

[4] "Habilité et fertilité de l'hybride *G. urbanum* L. × *G. rivale* L." *Comptes rendus Acad. Sci.* 1920, T. 170, p. 1284. Paris.

G. intermedium, Stock plant B. Nith Valley, Dumfriesshire.
G. intermedium × *rivale*, Stock plant F. Ufton Wood, Warwickshire.

Geum urbanum Linn. Stock plant A.

Stem. Up to 8 dm. high.

Anthocyanin. A trace, greenish red in pedicels and calyx segments.

Hairs. Plant sparingly hairy, with a few white gland tipped hairs on peduncles, pedicels and calyx segments.

Leaf. Radical leaves stalked, pinnate and lyrate; stem leaves ternate or three-lobed, stipules of lower cauline leaves very large, foliaceous, rounded, lobed and toothed. Average size 3·5 cm. long, 3·5 cm. broad; 3 cm. long, 2·8 cm. broad[1].

Calyx. Gamosepalous, sepals 10, reddish green, spreading and reflexing. Inner segments triangular-acuminate, outer ones very small linear-lanceolate.

Corolla. Polypetalous, petals 5, spreading, obovate-elliptical, rounded at apex, no claw at base (Pl. XIII, fig. 1).

Androecium. Filaments yellowish green, turning yellowish pink with age, ripe anthers orange.

Gynaecium. Styles bright red, upper joint of style 2 mm., glabrous above, then clothed with a few short hairs to the articulation, glabrous below, with a few minute hairs above achene and a very few minute white-tipped glandular hairs Lower joint 8 mm.

Petal colour. Pale lemon, slightly tinging pink on underside.

Flower habit. Very slightly drooping.

Fruit. Achenes compressed, narrowly ellipsoid, plumose and hispid.

Carpophore. None.

Maturity. Later than *rivale*.

Geum rivale Linn. Stock plant C.

Stem. Up to 6 dm. high.

Anthocyanin. A little in upper part of stem, purplish, much in peduncles, pedicels and calyx segments.

Hairs. Plant sparingly hairy, densely covered with red-tipped glandular hairs on peduncles, pedicels and calyx segments.

Leaf. Radical leaves stalked, pinnate and lyrate; stem leaves ternate or three-lobed, stipules of lower cauline leaves very small, ovate and coarsely toothed. Average size 1 cm. long, 4 mm. broad; 1·1 cm. long, 5 mm. broad.

[1] The two sets of measurements refer to the two stipules of one pair.

Calyx. Gamosepalous, sepals 10, purplish, erect, adpressed to receptacle after flowering; inner segments triangular-acuminate, outer segments small linear-lanceolate.

Corolla. Polypetalous, petals 5, erect, limb broadly oblate, retuse, abruptly contracted into a long narrowly wedge-shaped claw at base (Pl. XIII, fig. 2).

Androecium. Filaments greenish white, turning pinkish with age; ripe anthers deep lemon.

Gynaecium. Styles purplish red, upper joint of style 6 mm., glabrous above, then clothed with plumose hairs to the articulation, glabrous below, plumose above achene with many red-tipped glandular hairs. Lower joint 9 mm.

Flower colour. Pinkish brown.

Flower habit. Pendulous.

Fruit. Achenes compressed, narrowly ellipsoid, plumose and hispid.

Carpophore. 5 mm.

Maturity. Earlier than *urbanum*.

Geum intermedium Willd. haud Ehrh. Stock plant B.

Stem. Up to 8 dm. high.

Anthocyanin. A medium amount, reddish purple, in peduncles, pedicels and calyx segments.

Hairs. Plant sparingly hairy, with numerous red-tipped glandular hairs on peduncles, pedicels and calyx segments.

Leaf. Radical leaves stalked, pinnate and lyrate; stem leaves ternate or three-lobed; stipules of lower cauline leaves medium, foliaceous, rounded, deeply lobed and toothed. Average size 2·4 cm. long, 2·1 cm. broad; 1·9 cm. long, 1·5 cm. broad.

Calyx. Gamosepalous, sepals 10, reddish, semi-erect to semi-spreading, adpressed to receptacle after flowering; inner segments triangular-acuminate, outer segments small linear-lanceolate.

Corolla. Polypetalous, petals 5, semi-erect, to semi-spreading, roundish obovate, rounded at apex, narrowed into a short wedge-shaped claw at base.

Androecium. Filaments yellowish green turning yellowish pink with age; ripe anthers orange.

Gynaecium. Styles bright red; upper joint of style 4 mm., glabrous above, then clothed with plumose hairs to the articulation, glabrous below, sparingly plumose above achene with a few red-tipped glandular hairs. Lower joint 9 mm.

Flower colour. Orange, under surface veined and flushed pink.

Flower habit. Pendulous.

Fruit. Achenes compressed, narrowly ellipsoid, plumose and hispid.

Carpophore. 2 mm.

Maturity. As *rivale.*

Geum intermedium × *rivale.* Stock plant F.

Stem. Up to 6·4 dm. high.

Anthocyanin. With little in upper part of stem, purplish, much in peduncles, pedicels and calyx segments.

Hairs. Plant sparingly hairy, densely covered with red-tipped glandular hairs on peduncles, pedicels and calyx segments.

Leaf. Radical leaves stalked, pinnate and lyrate; stem leaves ternate or three-lobed, stipules of lower cauline leaves small, ovate, lobed and coarsely toothed. Average size 1 cm. long, 5 mm. broad; 1·2 cm. long, 6 mm. broad.

Calyx. Gamosepalous, sepals 10, purplish, erect, adpressed to receptacle after flowering; inner segments triangular-acuminate, outer segments small linear-lanceolate.

Corolla. Polypetalous, petals 5, erect, oblate, slightly retuse, abruptly contracted into a short wedge-shaped claw at base (Pl. XIII, fig. 3).

Androecium. Filaments greenish white, turning pink with age; ripe anthers lemon.

Gynaecium. Styles purplish red, upper joint of style 4 mm., glabrous above, then clothed with plumose hairs to the articulation, glabrous below, plumose above achene with many red-tipped glandular hairs. Lower joint 7·5 mm.

Flower colour. Deep buff, veined and flushed rose on upper and lower surfaces.

Flower habit. Pendulous.

Fruit. Achenes compressed, narrowly ellipsoid, plumose and hispid.

Carpophore. 6 mm.

Maturity. As *rivale.*

Breeding results.

The characters studied are as follows:

1. Presence and absence of anthocyanin.
2. Glands on peduncles, pedicels and calyx segments.
3. Petal shape.
4. Petal claw.

5. Hairs above stylar articulation.
6. Hairs on style immediately above achene.
7. Glands above achene.
8. Colour of glands above achene.
9. Petal colour.
10. Flower habit.
11. Length of carpophore.
12. Maturity.

Below are the characters contrasted in the two species:

	Geum urbanum.	*Geum rivale.*
1.	Anthocyanin—absent.	Anthocyanin—present, purplish.
2.	Glands on peduncles—few.	Glands on peduncles—many.
3.	Petal shape—obovate-elliptical.	Petal shape—broadly oblate, retuse.
4.	Petal claw—none.	Petal claw—long, wedge-shaped.
5.	Hairs above articulation—short.	Hairs above articulation—plumose.
6.	Hairs on style above achene—short.	Hairs on style above achene—plumose.
7.	Glands above achene—few.	Glands above achene—many.
8.	Colour of glands—white.	Colour of glands—red.
9.	Petal colour—pale lemon.	Petal colour—pinkish brown.
10.	Flower habit—almost erect.	Flower habit—pendulous.
11.	Carpophore—absent.	Carpophore—present.
12.	Maturity—later than *rivale*.	Maturity—earlier than *urbanum*.

× *D.* 62. Geum urbanum *Stock plant A* ♀ × rivale *Stock plant C* ♂.
(Plate XII.)

A generation of forty-four plants was raised quite indistinguishable from natural hybrids observed in the wild, and comparable with *G. intermedium* B already described.

Analysis of characters[1].

1. *Anthocyanin.* All 44 plants identical, reddish purple.

2. *Glands on peduncles, pedicels and calyx segments.* Few, 33. Many, 11.

[1] It was not always possible to score every plant for all the characters studied. The counts therefore, in some cases, do not agree with the number of plants in the generations.

3. *Petal shape* (Pl. XIV, fig. 4). Identical, roundish obovate, rounded at apex, 44.

4. *Petal claw.* Identical, with short wedge-shaped claw, 44.

5. *Hairs above stylar articulation.* Identical, plumose, 44.

6. *Hairs on style immediately above achene.* Identical, sparingly plumose, 44.

7. *Glands above achene.* Absent, 39. Very few, 5.

8. *Colour of glands.* Identical, red-tipped, 44.

9. *Petal colour.* Identical, orange, under surface veined and flushed pink, 44.

10. *Flower habit.* Identical, pendulous, 44.

11. *Length of carpophore.* Absent, 39. 1 mm. 4. 2 mm. 1.

12. *Maturity.* Identical, as *rivale*, 44.

Comments on characters analysed.

From the above figures it will be seen that although *G. intermedium* appears to be quite intermediate between its parents, it is not really so. The only intermediate characters amongst the twelve analysed are 3, 4 and 9, while 1, 5, 6, 8, 10 and 12 are completely dominant *rivale* characters. In 2 and 11 the *urbanum* character appears in the majority of plants, in 2 the simple 3 : 1 ratio is obtained, in 11 the ratio is 7·8 : 1. 7 shows loss of a character, in *urbanum* the glands above the achene are few, in *rivale* many; thirty-nine out of the forty-four plants scored have none.

Taking all the characters into account *rivale* is the more dominant parent. It would perhaps be better if petal colour was classed in a separate group, since, as shown by Weiss, it is due to the inheritance of distinct factors from each parent, whose resultant characters give together a blending result in F_1.

× *D* 59. Geum intermedium *Stock plant B selfed.*

An F_2 generation was raised consisting of sixty-three plants. On looking over these individuals it was apparent that a considerable amount of segregation had taken place, also that distinct types of plants had appeared. It was possible definitely to divide these into four groups which were lettered *S*, *T*, *Y*, *Z*, but the analysis of the characters was taken for the whole generation irrespective of the groups.

Group S. One plant rather like *rivale* in appearance. Stipules of lower cauline leaves rather small, foliaceous, rounded, lobed and toothed. Average size 1·5 cm. long, 1·2 cm. broad; 1·5 cm. long, 1·1 cm. broad.

A plant resembling this individual, but with rather paler petals, was found in the wild and might have been taken for a pale form of *rivale*.

Group T. Five plants, with small erect to semi-spreading flowers. Stipules of lower cauline leaves rather small, foliaceous, rounded, lobed and toothed. Average size 1·6 cm. long, 1 cm. broad; 1·7 cm. long, 1·1 cm. broad. Nearer *intermedium* than *rivale*.

Group Y. Seven plants, with small semi-erect flowers never spreading, stipules of lower cauline leaves rather small, foliaceous, rounded, lobed and toothed. Average size 1·5 cm. long, 9 mm. broad; 1·1 cm. long, 6 mm. broad. Nearer *rivale* than *intermedium*.

Group Z. Fifty plants, with large semi-erect to semi-spreading flowers. Stipules of lower cauline leaves rather small, foliaceous, rounded, lobed and toothed. Average size 1·5 cm. long, 9 mm. broad; 1·5 cm. long, 8 mm. broad. Near *intermedium*.

Analysis of characters.

1. *Anthocyanin*. Absent, 9. Much, 54.
2. *Glands on peduncles, pedicels and calyx segments*. Few, 3. Many, 49.
3. *Petal shape*. Oblate, 6. Roundish obovate, 16; broadly obovate, 23; very broadly obovate, 18.
4. *Petal claw*. Very short, 15. Short, 48.
5. *Hairs above stylar articulation*. Short, 21. Plumose, 37.
6. *Hairs on style immediately above achene*. Short, 0. Plumose, 56.
7. *Glands above achene*. Few, 41. Many, 13.
8. *Colour of glands*. White-tipped, 9. Red-tipped, 54.
9. *Petal colour*. Orange, veined pink above, 42. Buff, veined pink above, 18. Lemon, veined and flushed pink on under surface, 2. Primrose, 1.
10. *Flower habit*. Drooping, 5. Pendulous, 58.
11. *Length of carpophore*. Absent, 39. 1 mm. 11. 2 mm. 8. 3 mm. 4. 4 mm. 1.
12. *Maturity*. As *rivale*.

Comments on characters analysed.

From selfing *Geum intermedium*, the ratios obtained for the various characters in many cases do not conform to simple Mendelian expectation.

1. The *rivale* character appeared in the majority of plants, fifty-four had much anthocyanin and nine none. The expected ratio was 3 : 1,

actually it was 6 : 1. From the data obtained *rivale* is seen to be either dominant or predominant in several of the characters analysed. It is suggested that this predominance has inhibited the showing of the expected ratio. A similar statement holds for 8, where a ratio of 6 : 1 was also obtained.

2. No Mendelian ratio occurs, the *rivale* character for many glands being almost completely dominant, only three plants in the generation being sparingly glandular.

3. We have here four types of petal shapes. There were no plants with petals that agree in shape with those of *urbanum*, six that were oblate in outline as *rivale*, sixteen roundish obovate as *intermedium*, twenty-three broadly obovate and eighteen very broadly obovate. By classing together the obovate type of petal there is a total of fifty-seven against six oblate. No simple Mendelian ratio obtained.

4. There were no plants in the generation without a claw as in *urbanum*, and plants with the long claw of *rivale* were also absent, forty-eight were as *intermedium* with a short claw and fifteen had a very short one. The ratio obtained is 3·2 : 1, the *intermedium* character appearing in the majority of the plants, but it is a matter of degree, and rather difficult to score.

5. If the generation had been larger it is probable that a 3 : 1 ratio would have resulted, that actually obtained is 1·8 : 1, the *rivale* character appearing in the majority of plants.

6. The *rivale* character for plumose hairs is completely dominant as it was in the F_1. It is quite inexplicable why there were no plants with short hairs, while twenty-one had short hairs above the stylar articulation. This is a very clear cut character, *urbanum* having short, and *rivale* plumose hairs.

7. This is the first instance of an *urbanum* character appearing in most of the plants, the ratio for few to many glands being 3·2 : 1.

8. See 1.

9. For petal colour there are several factors involved and this generation and the subsequent ones are too small to give any satisfactory explanation of the results obtained.

10. The *rivale* character is almost completely dominant, only five plants out of the sixty-three having drooping flowers.

11. In eleven plants it was just possible to measure the carpophore, in thirty-nine it was absent; these together give a total of fifty, against thirteen with the carpophore ranging from 2 mm. to 4 mm., giving a ratio of 3·8 : 1, the *urbanum* character appearing in the majority of plants.

12. All the plants flowered before *urbanum*, the early maturity of *rivale* being completely dominant as it was in the F_1 generation.

× *D* 60. Geum intermedium *Stock plant B* ♀ × rivale *Stock plant C* ♂.

There were forty plants in the generation, the *rivale* characters strongly predominating, as would be expected from the history of this cross and from the results obtained in the F_1 and F_2 generations which gave a preponderance of dominant *rivale* characters. The fifteen plants with pinkish brown petals were superficially very like *rivale*, indeed any of the plants in this generation might easily be mistaken for such in the field. No distinct types stood out as in the F_2 generation, the appearance of the plants in the beds giving the impression that they were a batch of *rivale*, no segregation having taken place comparable with that obtained from back-crossing *intermedium* with *urbanum*. For petal shape it was possible to divide the plants into two groups, *O* and *Q*.

Group O. Ten plants, with obovate petals, stipules of lower cauline leaves small, ovate, lobed and coarsely toothed. Average size, 9 mm. long, 3 mm. broad; 1·2 cm. long, 5 mm. broad.

Group Q. Thirty plants with oblate petals, stipules of lower cauline leaves small, ovate, lobed and coarsely toothed. Average size 1·2 cm. long, 4 mm. broad; 9 mm. long, 3 mm. broad.

Analysis of characters.

1. *Anthocyanin*. Absent, 0. Much, 40.
2. *Glands on peduncles, pedicels and calyx segments*. Few, 1. Many, 39.
3. *Petal shape* (Pl. XIV, fig. 5). Roundish obovate, 2; broadly obovate, 8. Oblate, 2; broadly oblate, 28.
4. *Petal claw*. Short, 13. Long, 27.
5. *Hairs above stylar articulation*. Short, 0. Plumose, 38.
6. *Hairs on style immediately above achene*. Short, 0. Plumose, 38.
7. *Glands above achene*. Few, 20. Many, 18.
8. *Colour of glands*. White-tipped, 0. Red-tipped, 40.
9. *Flower colour*. Pinkish brown, 15. Deep buff, 10. Pale buff, 14. Orange, 1. All veined and flushed pink on upper and under surfaces.
10. *Flower habit*. Drooping, 0. Pendulous, 40.
11. *Length of carpophore*. Absent, 7. 1 mm. 5. 2 mm. 4. 3 mm. 5. 4 mm. 9. 5 mm. 5. 6 mm. 5.
12. *Maturity*. As *rivale*.

Comments on characters analysed.

1. All the plants had much anthocyanin in peduncles, pedicels and calyx segments; *rivale* character dominant.

2. The glands fluctuated slightly in number on different plants, one had to be scored as "few," but no individual had the few glands of *urbanum*; *rivale* character dominant.

3. There were, classing together the roundish obovate and the broadly obovate, the oblate and the broadly oblate, two types of petal shapes, thirty agreeing in outline with *rivale* and ten with *intermedium*, giving a ratio of 3 : 1, the *rivale* character appearing in the majority of plants.

4. For this character *rivale* is dominant in twenty-seven plants which had a long claw, while thirteen had the short claw of *intermedium*, giving a ratio of 2 : 1. If the generation had been larger, it is probable that a 3 : 1 ratio would have been obtained.

5. *Rivale* character completely dominant.

6. *Rivale* character completely dominant.

7. Here segregation has taken place, twenty plants having few and eighteen many glands, giving a ratio of 1 : 1. As *intermedium* is heterozygous, this is as would be expected. The *rivale* character for many glands was not dominant in F_1 or F_2 and consequently has not suppressed the expected ratio.

8. No segregation, the *rivale* character dominant.

9. Fifteen plants had petals indistinguishable from *rivale* in colour, twenty-four near *rivale*, and only one with the orange colouring of *intermedium*; *rivale* character predominant.

10. *Rivale* character dominant.

11. Twenty-eight plants had a carpophore from 2 mm. to 6 mm. long. By classing together the plants that had no carpophore and those with a carpophore of 1 mm. as was done in the F_2 generation a total of twelve was obtained. This gives a ratio of 2·3 : 1, an approximation to a 3 : 1, with the *rivale* character appearing in the majority of plants.

12. *Rivale* character dominant.

× *D* 61. Geum intermedium *Stock plant B* ♀ × urbanum *Stock plant A* ♂.
Fifty-five plants.

× *D* 64. Geum urbanum *Stock plant A* ♀ × intermedium *Stock plant B* ♂.
Thirty-nine plants.

As the results were identical from these two crosses, it was thought desirable to add them together for analysis; there were, therefore, ninety-four plants considered as a generation.

With the exception of four plants, two of *intermedium* and two of *urbanum*, the whole generation was superficially very like *urbanum*, indeed in the field many of them would have been passed for *urbanum*. The plants were divided into four groups, *L*, *M*, *H* and *G*.

Group L. Fifty-two plants with petals varying in shape from obovate-elliptical to very broadly obovate, calyx not reflexing, stipules of lower cauline leaves medium, foliaceous, rounded, lobed and toothed. Average size 2·1 cm. long, 2·3 cm. broad; 2·6 cm. long, 2·7 cm. broad.

Group M. Thirty-eight plants with petals as in Group *L*, calyx reflexing, stipules of lower cauline leaves medium, foliaceous, rounded, lobed and toothed. Average size 2·2 cm. long, 2·2 cm. broad; 2·6 cm. long, 2·1 cm. broad.

Group H. Two plants, typical *intermedium*, petals roundish obovate, stipules of lower cauline leaves medium, foliaceous, rounded, lobed and toothed. Average size 2·4 cm. long, 2·1 cm. broad; 2·4 cm. long, 2·1 cm. broad. One from each reciprocal cross.

Group G. Two plants, typical *urbanum*, petals obovate-elliptical, stipules of lower cauline leaves large, foliaceous, rounded, lobed and toothed. Average size 2·7 cm. long, 2·5 cm. broad; 2·7 cm. long, 2·7 cm. broad. One from each reciprocal cross.

Analysis of characters.

1. *Anthocyanin*. Absent, 42. Little, 50. Medium, 2.
2. *Glands on peduncles, pedicels and calyx segments*. None, 1. Few, 61. Medium, 32.
3. *Petal shape*. Obovate-elliptical, 48. Roundish obovate, 14; broadly obovate, 14; narrowly obovate, 18.
4. *Petal claw*. Absent, 60. Short, 34.
5. *Hairs above stylar articulation*. Short, 51. Short plumose, 41. Plumose, 2.
6. *Hairs on style immediately above achene*. Absent, 27. Short, 6. Sparingly plumose, 61.
7. *Glands above achene*. Absent, 43. Few, 48. Many, 0.
8. *Colour of glands* (scored from calyx segments). White-tipped, 41. Red-tipped, 52.
9. *Flower colour*. Lemon, 25. Orange veined pink, 24. Lemon veined pink, 27. Orange, 18.
10. *Flower habit*. Very slightly drooping, 92. Pendulous, 2[1].
11. *Length of carpophore*. Absent, 94.
12. *Maturity*. As *urbanum*, 92. As *rivale*, 2[1].

[1] These characters are derived from the two plants of *intermedium* in the generation.

Comments on characters analysed.

1. There were forty-two plants with no anthocyanin as *urbanum*, two with the medium amount of *intermedium* and fifty in which a little developed, much more than the slight trace which may be found in *urbanum*, which when found is never, so far as I have observed, correlated with red glands. The ratio obtained is an approximation to 1 : 1.

2. Sixty-one plants had few glands, thirty-two had a medium number and one none. The *urbanum* character appeared in the majority of plants, the ratio being approximately 2 *urbanum* : 1 *intermedium*.

3. There were forty-eight plants with obovate-elliptical petals and by classing together those with roundish, broadly and narrowly-obovate petals a total of forty-six is obtained giving a ratio of 1 : 1.

4. In sixty plants the claw was absent, and in thirty-four short, giving an approximate ratio of 2 *urbanum* : 1 *intermedium*.

5. The ratio here obtained agrees closely to a 1 : 1, there being fifty-one plants with short and forty-three with plumose hairs, but attention is called to a new character, viz. a short type of plumose hair, very distinct from the plumose hairs found in *rivale* and *intermedium*. It might be suggested that a double dose of *urbanum* modifies the full development of the plumose character.

6. There were sixty-one plants with sparingly plumose hairs, six with short hairs but not so minute as those of *urbanum* and twenty-seven from which the hairs were altogether absent, showing the loss of a character. The *intermedium* character appeared in the majority of plants.

7. Forty-eight plants had the few glands of *urbanum*; in forty-three they were absent. The ratio obtained is approximately 1 : 1, but the absence of glands shows loss of a character.

8. There were forty-one plants with white-tipped glands and fifty-two with red-tipped—an approximation to a 1 : 1 ratio.

9. Twenty-five plants had petal colour as *urbanum* and twenty-four as *intermedium*; further, there were twenty-seven plants with lemon veined pink petals and eighteen with orange petals. No simple Mendelian ratio obtained.

10. The *urbanum* character is predominant, only two plants having pendulous flowers.

11. The *urbanum* character dominant.

12. The *urbanum* character is predominant, two plants only flowering earlier than *urbanum*.

× *D* 66. *Collected back-cross* Geum intermedium × rivale *Stock plant F. Selfed.*

The generation of fifty-four plants obtained from × *D* 66 gives results that are of great importance and interest. No segregation took place in the ordinary sense of the word, the plants were like their parent, only minor fluctuations being observed, such as are to be found within the range of a species. This result, and that obtained by back-crossing *intermedium* with *rivale*, must be taken into account when studying a wild population. Without the data obtained from controlled work, considerable confusion must arise in attempting to define true *rivale*, and in separating it from plants that are of back-cross origin.

Analysis of characters.

1. *Anthocyanin.* Absent, 0. Much, 54.
2. *Glands on peduncles, pedicels and calyx segments.* Few, 0. Many, 54.
3. *Petal shape* (Pl. XIV, fig. 6). Broadly oblate, 54.
4. *Petal claw.* Short, 54. Long, 0.
5. *Hairs above stylar articulation.* Short, 0. Plumose, 54.
6. *Hairs on style immediately above achene.* Short, 0. Plumose, 54.
7. *Glands above achene.* Few, 0. Many, 54.
8. *Colour of glands.* White-tipped, 0. Red-tipped, 54.
9. *Flower colour.* Pale buff, veined and flushed rose, 23. Deep buff, veined and flushed rose, 31.
10. *Flower habit.* Drooping, 0. Pendulous, 54.
11. *Length of carpophore.* Ranging from 4 mm. to 11 mm.
12. *Maturity.* As *rivale.*

Comments on characters analysed.

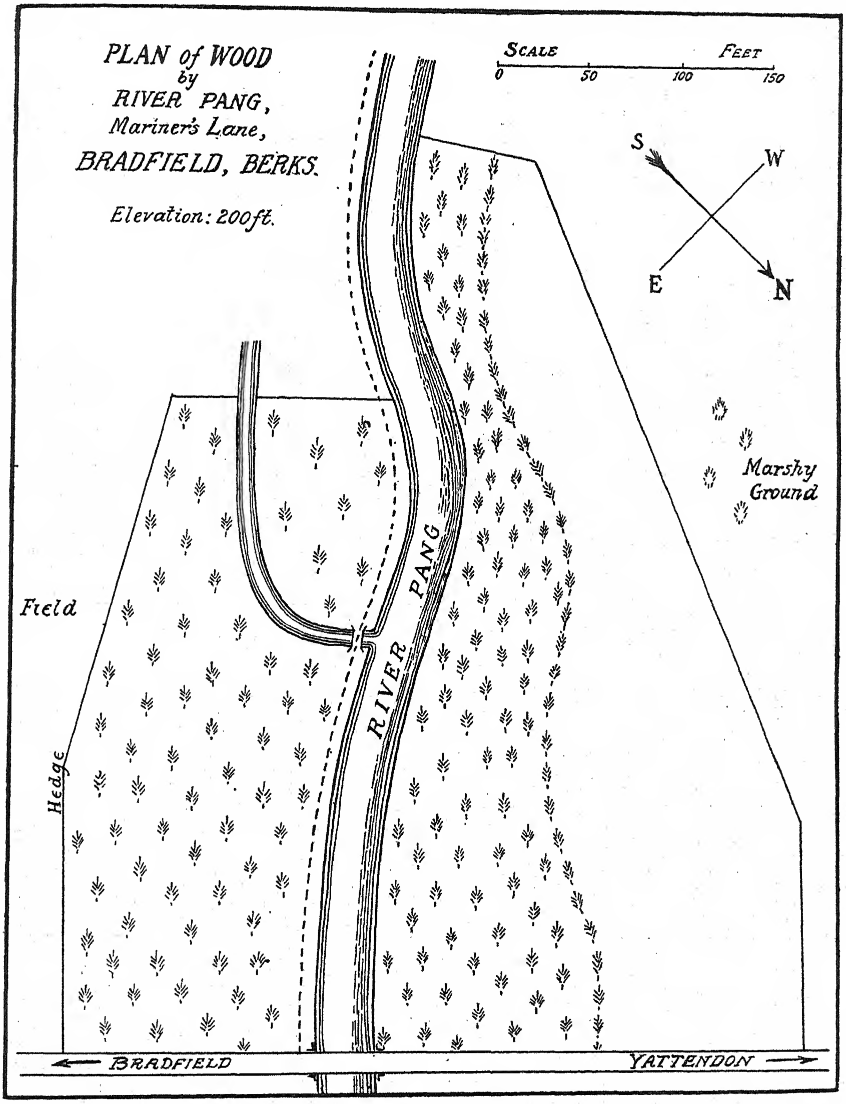
As will be seen from the above analysis the characters studied agree very closely with those of the parent.

Field work.

Beside the controlled breeding work, a very careful study has been made of a *Geum* population growing in a wood at Bradfield, Berks., V.C. 22 (Plan). The results obtained from this examination are of great interest, and are strengthened by the facts derived from the experimental work.

The part of the wood on the north-west side of the River Pang had been cut about 1925, and is composed of *Salix fragilis* Linn., *S. cinerea*

Linn., *S. viminalis* Linn., *S. purpurea* Linn. forma *Lambertiana* (Smith), *S. aurita* × *cinerea* (*S. lutescens* A. Kerner), *S. aurita* × *viminalis* (*S. fruticosa* Dölt), *S. fragilis* × *triandra* (*S. alopecuroides* Tausch),



Betula pubescens Ehrhart, *Populus tremula* Linn. var., *Alnus rotundifolia* Mill., *Fraxinus excelsior* Linn., *Ulmus campestris* Linn., *Ulmus major* Smith (*U. montana* × *nitens*), *Cornus sanguinea* Linn., *Crataegus mono-*

gyna Jacq., *Prunus spinosa* Linn., *Rosa stylosa* Desvaux. var. *systyla* Baker, *R. arvensis* Huds., *R. dumetorum* Thuillier, *Cnicus palustris* Willd., *Rumex glomeratus* Schreb., *Hypericum perforatum* Linn., *Mercurialis perennis* Linn., *Ranunculus repens* Linn., *Hedera Helix* Linn., *Urtica dioica* Linn., *Caucalis Anthriscus* Huds., *Epilobium montanum* Linn., *E. hirsutum* Linn., *Trifolium repens* Linn., *Arctium minus* Bernh., *Lathyrus pratensis* Linn., *Polygonatum multiflorum* Alt., *Iris Pseudacorus* Linn., *Crepis capillaris* Wallr., *Stellaria Holostea* Linn., *Scrophularia aquatica* Linn., *Spiraea Ulmaria* Linn., *Eupatorium cannabinum* Linn., *Angelica sylvestris* Linn., *Clinopodium vulgare* Linn., *Juncus effusus* Linn., *Carex riparia* Curt., and *Bromus gigantea* Linn.

The part on the south-east side of the river is composed of *Alnus rotundifolia* Mill., approximately 30 ft. in height giving considerable shade, *Salix cinerea* Linn., *S. fragilis* × *triandra* (*S. alopecuroides* Tausch), *S. caprea* × *viminalis* (*S. mollissima* Smith), *Betula pubescens* Ehrhart, *Prunus cerasifera* Ehrhart, *Euonymus europaeus* Linn., *Rosa dumetorum* Thuillier forma *semiglabra* W.-Dod., *Corylus Avellana* Linn., *Solanum Dulcamara* Linn., *Calystegia sepium* Br., *Urtica dioica* Linn., *Spiraea Ulmaria* Linn., *Eupatorium cannabinum* Linn., *Scrophularia aquatica* Linn., *Iris Pseudacorus* Linn., *Mercurialis perennis* Linn., *Stachys sylvatica* Linn., *Stellaria Holostea* Linn., *S. aquatica* Scop., *Epilobium hirsutum* Linn., *Symphytum officinale* Linn., *Carex riparia* Curt., *Phalaris arundinacea* Linn., and *Deschampsia caespitosa* Beauv.[1]

On the north-west side the wood can be divided into two zones, wet and dry, the dividing line being roughly half-way between the river and the hedge. Along the hedge are found plants of *Geum urbanum*, *urbanum* × *intermedium*, segregates from *intermedium*, and a few plants of *intermedium* × *rivale*. In the dry zone appear *intermedium*, *intermedium* × *urbanum*, segregates from *intermedium*, and a number of plants of *intermedium* × *rivale*. At the edge of the wet zone are found a few plants of *intermedium*, *intermedium* × *urbanum*, and many plants of *intermedium* × *rivale*. The wet zone contains plants of *rivale* and *rivale* × *intermedium* only, but the predominant population is the back-cross (Pl. XV, fig. 7). Growing along the hedge on the north-east side of the wood nearly to the river are a few plants of *G. urbanum*. The plants of back-cross origin agree very closely with those obtained from the controlled work; the back-crosses of *urbanum* × *intermedium* origin have calyces adpressed or reflexing, corollas erect, semi-erect or spreading, the colour of the petals varying from pale lemon to yellow. Towards the

[1] The lists given are of the principal species observed on 5 September, 1929.

west side of the wood, close to the edge, are a colony of plants of *urbanum* × *intermedium* parentage without anthocyanin, with reflexing calyces, and lemon petals. The plants of *intermedium* seen are typical of the plant obtained by crossing *urbanum* with *rivale*.

The most interesting plants studied were the *rivale* × *intermedium* group, the calyces of which are as *rivale*, and petal shape some as *rivale*, some oblate but not retuse, others rounded. The colour varies from buff flushed pink to deep buff veined pink.

In the portion of the wood on the south-east of the river no plants of *urbanum rivale* or *intermedium* are to be found, and most of the population, which is considerable, consists of *rivale* × *intermedium* (Pl. XV, fig. 8). Growing amongst these are a few plants with semi-spreading calyces and corollas, and in one place a colony of about twenty of such plants, with colour of petals lemon, slightly veined red, or pinkish (Pl. XV, fig. 9). The plants with lemon petals have no anthocyanin and the glands are white; the ones with the pinkish petals have less anthocyanin than *rivale*, but the glands are red. Outside the wood there are plants of *urbanum* within pollinating distance; it is suggested that the plants with the open flowers are *rivale* × *intermedium* × *urbanum*, and the fact that such plants are found lends additional support to the plants mentioned above being *rivale* × *intermedium*. That *urbanum* and *intermedium* are not to be seen in this part of the wood is, I think, explained by the fact that it is very dense and wet, and not a suitable habitat for these plants. A rough field adjoins the wood on the south-east, *rivale* occurs here, but the majority of the plants are of *rivale* × *intermedium* origin. The colour of the petals of such plants varies from pale lemon flushed pink, buff more or less flushed pink, to white flushed pink.

From the study of these three populations it at once becomes apparent that the back-cross *rivale* × *intermedium* is having a marked influence, and, in this locality at any rate, it would appear that in the near future it will completely replace true *rivale*, indeed in the wood on the south-east of the river it has already done so.

SUMMARY.

From the study of a large number of individuals of *Geum intermedium* both in the Experimental Ground at Potterne and in the wild, it seems that the F_1 plants resulting from a cross between *G. urbanum* and *G. rivale* are always identical, with exceptions only in the number of glands and length of carpophore, and that in reality the F_1 is not intermediate between the two species. In the characters I have studied only three

are intermediate, six show complete dominance of the *rivale* characters, and in three segregation takes place, the *urbanum* character appearing in the majority of plants in two cases, but in the third most of the plants show loss of a character, the glands above achene, common to both parents. On selfing *G. intermedium* segregation always takes place. Beside the account given of the F_2 generation obtained from × D. 59 six other F_1 plants from × D. 62 were selfed in order to see if it were possible to find a plant that might breed true, but in every case segregation took place. In the F_2 from × D. 59 four distinct types of plants appeared, none of them exactly comparable with either *urbanum*, *rivale* or *intermedium*. The results obtained from the back-crosses, × D. 60, × D. 61 and × D. 64 do not, for most characters, agree with the expected ratio of 1 : 1; in × D. 60 the *rivale* characters were, with one exception, either completely dominant or predominant. In × D. 61 and × D. 64, though in five cases a ratio of 1 : 1 was obtained, only in two was it what may be described as a straight ratio between the characters of the two species. Attention is also called to a new type of hair, short plumose, in × D. 61 and × D. 64. This is a new character and it is suggested that it has arisen through the inhibiting effect of a double dose of *urbanum*. In the same crosses many plants show the loss of two characters, hairs on style above achene, and glands above achene. The phenomenon of the appearance of new types on crossing has been recorded by Lotsy[1]. The occurrence of new types in offspring from *Centaurea* crosses has also been observed[2]. Winge[3] found that on back-crossing, the offspring are most like the parent used for the back-crosses. This is also my experience, but there is a vast difference in the behaviour of the back-crosses on selfing. Very considerable segregation takes place when a plant of the back-cross *intermedium* × *urbanum* is selfed, for example in the number of glands, colour of petals, and type of flowers, some having flowers near *urbanum*, with or without reflexing sepals, others near *intermedium*, with sepals reflexing, adpressed or spreading.

On selfing the back-cross *intermedium* × *rivale* a very different state of affairs is apparent, very little segregation taking place, so little, in fact, that without critical analysis, the plants might all be mistaken for *rivale*. Winge calls attention to this point, but suggests that back-crosses will again merge with the parent species. From field observations made

[1] *Evolution by Means of Hybridisation*, pp. 127–131.

[2] Marsden-Jones and Turrill MS.

[3] O. Winge, *Artkrydsningsproblemer i Planteriget*. Beretning om Nord. Jordbrugsforsk. Foren. tredie Kongres, Oslo, 1926.

Fig. 1. Fig. 2. Fig. 3.

Fig. 1

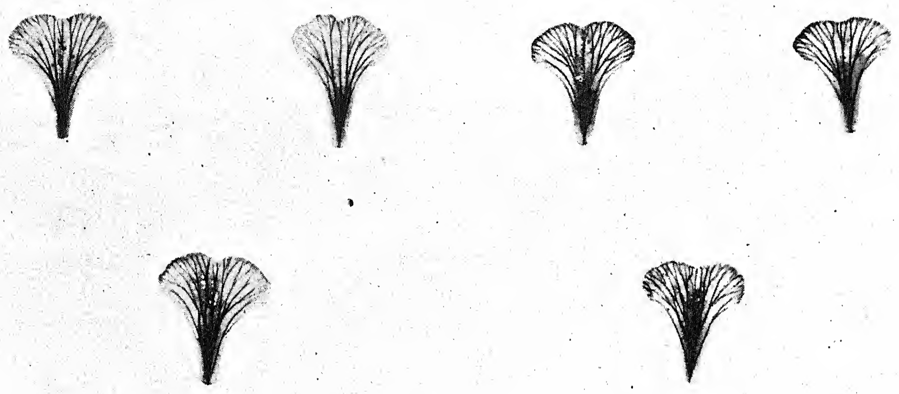


Fig. 2

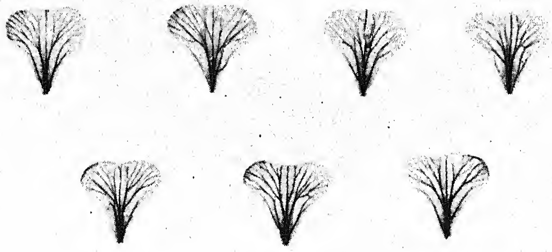


Fig. 3

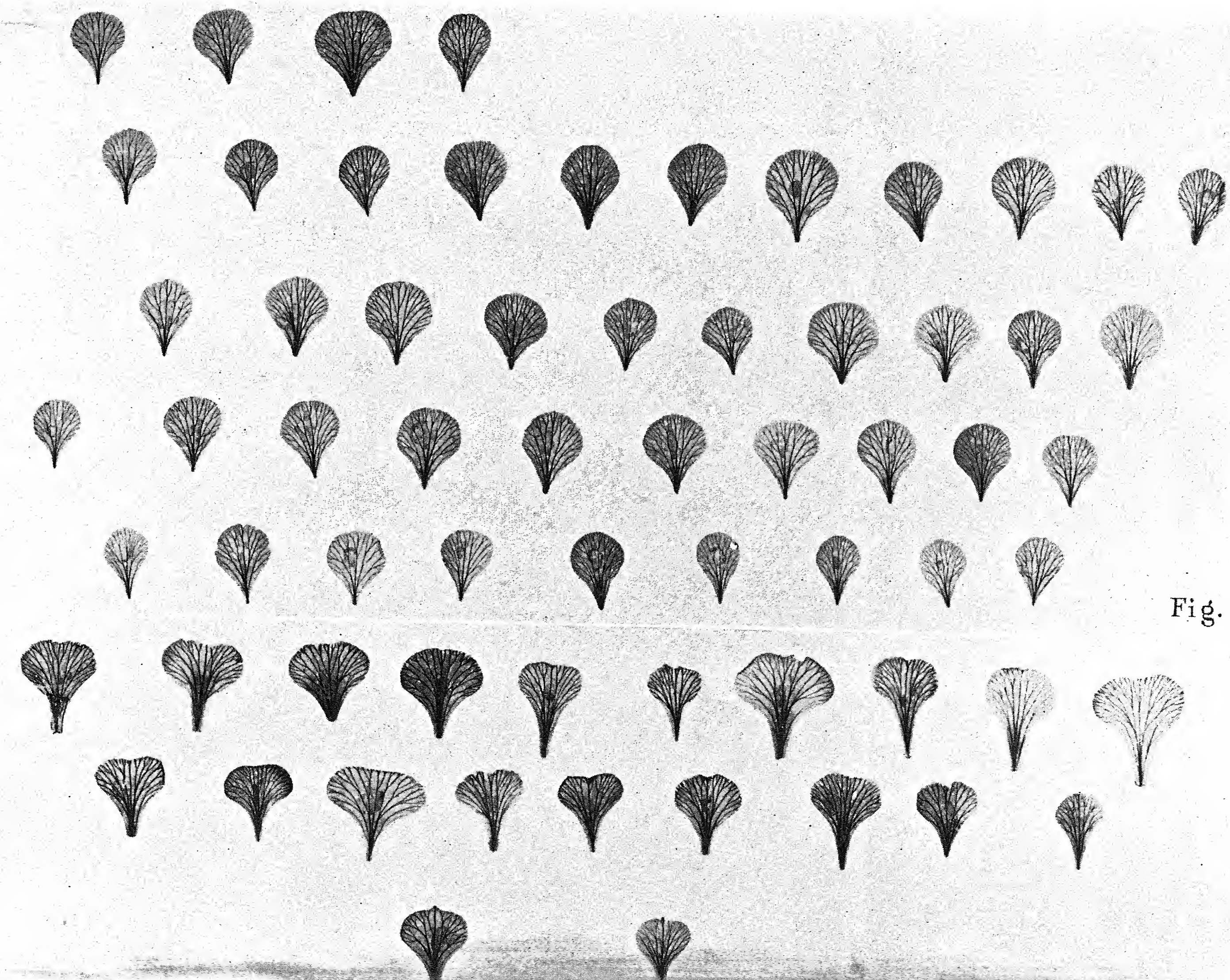


Fig. 4

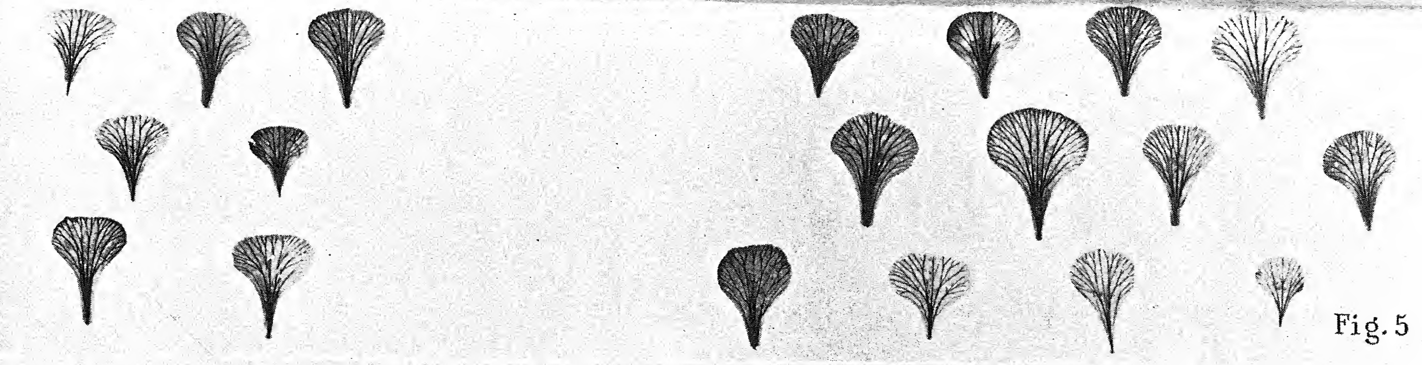


Fig. 5

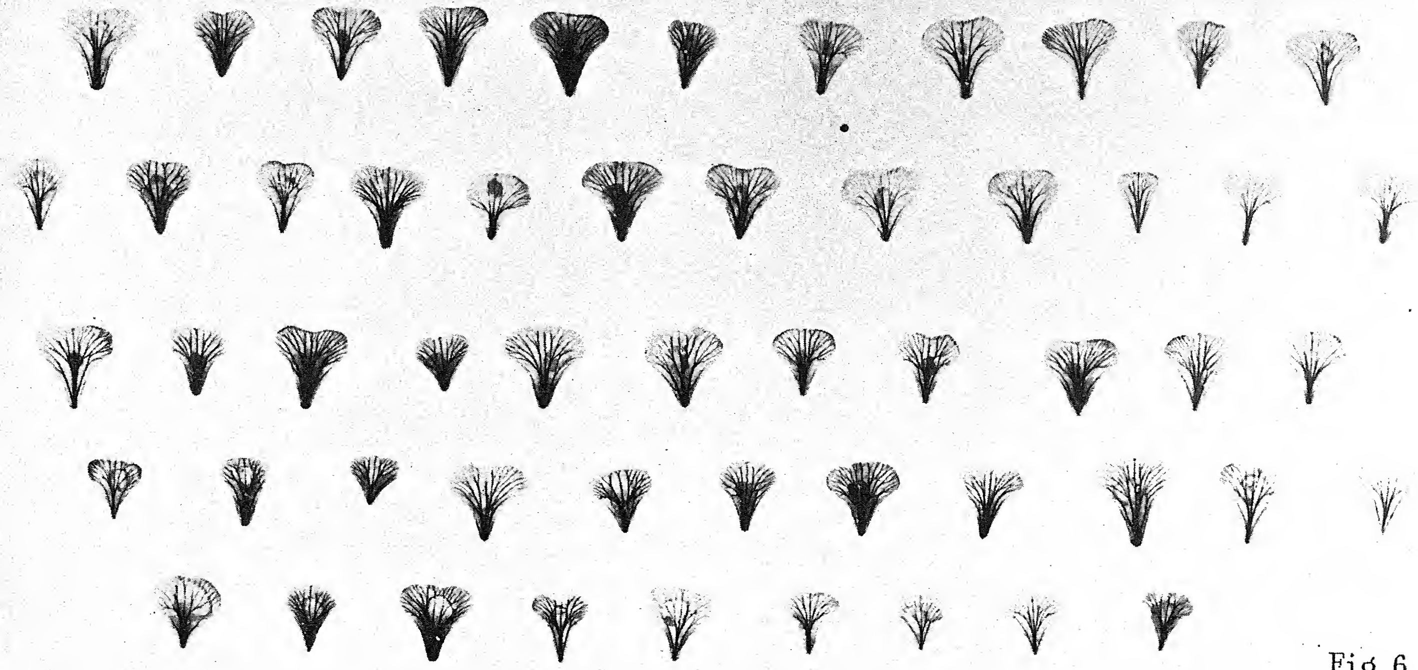


Fig. 6

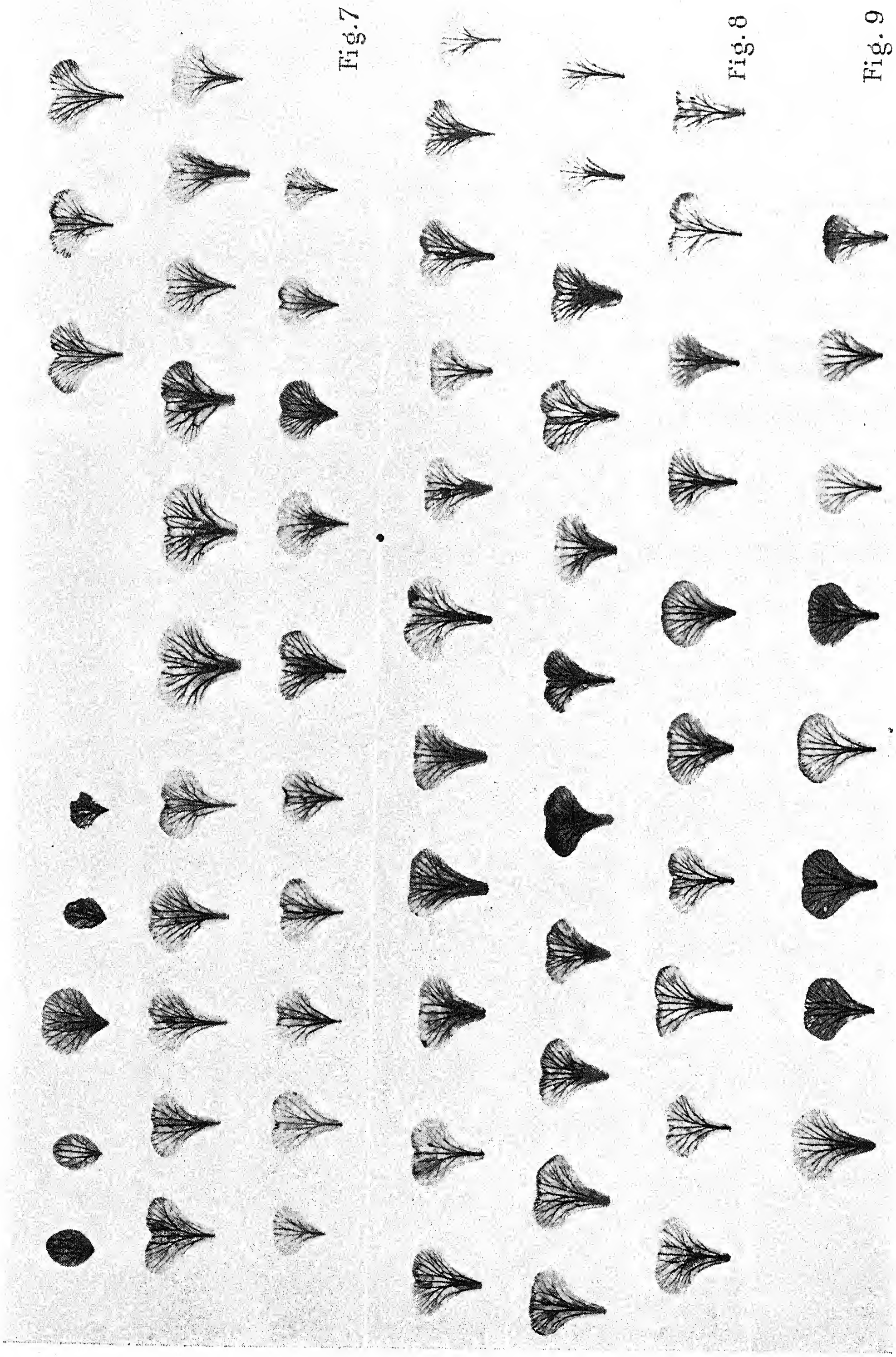


Fig. 7
Fig. 8
Fig. 9

in a wood at Bradfield, Berks., it would appear that in that locality at least this is not so, the back-cross having become stabilised and very largely replacing *rivale*, an example of a wild population of a new type arising from inter-specific hybridisation.

Samples of the material dealt with in this paper are preserved in the Herbarium at Kew.

EXPLANATION OF PLATES XII—XV.

Plate XII.

Geum intermedium Willd. haud Ehrh. Fig. 1 is of a plant produced artificially by crossing *G. urbanum* Stock plant A with *rivale* Stock plant C. Fig. 2. A flower $\times 1\frac{1}{2}$, with the sepals pressed back to show their shape and the position of the petals. Fig. 3. Achene $\times 4$.

Plate XIII.

Fig. 1. Petals of *G. urbanum* Linn. Stock plant A.
Fig. 2. Petals of *G. rivale* Linn. Stock plant C.
Fig. 3. Petals of *G. intermedium* × *rivale* Stock plant F.

Plate XIV.

Fig. 4. A petal from each plant in × D. 62, *G. urbanum* Stock plant A × *rivale* Stock plant C.

Fig. 5. A petal from each plant in × D. 60, *G. intermedium* Stock plant B × *rivale* Stock plant C.

Fig. 6. A petal from each plant in × D. 66, *G. intermedium* × *rivale* Stock plant F. Attention is called to the similarity in the shape of the petals.

Plate XV.

Fig. 7. Petals from separate plants collected at random on the north-west side of the wood at Bradfield, Berks. 1st row, left: *G. intermedium* × *urbanum* and segregates; right: *G. rivale*. 2nd and 3rd rows, *G. rivale* × *intermedium*. It will be seen that many of the petals in rows 2 and 3 can be matched with petals in Pl. XIV, figs. 5 and 6.

Fig. 8. Petals from separate plants collected at random on the south-east side of the wood at Bradfield, Berks. The similarity between these petals and those in Pl. XIV, figs. 5 and 6 is very striking.

Fig. 9. Petals from separate plants with spreading calyces and corollas collected on the south-east side of the wood at Bradfield, Berks.

STUDIES ON THE CREEPER FOWL.

I. GENETICS.

By WALTER LANDAUER and L. C. DUNN.

(*Storrs Agricultural Experiment Station, Storrs, Conn.*)

(With Plate XVI.)

THE so-called Creeper breed of fowls is characterised by a pronounced shortness of the extremities. Cutler has given a sufficient description of the external appearance and the morphology of the skeleton of such chickens. He found that all the bones of legs and wings are shortened, that the tibia usually is strikingly bent, and that the fibula is much better developed than in ordinary chickens.

In a preliminary report we were able to confirm Cutler's conclusion that the Creeper traits are dominant over the normal ones, and we advanced the tentative conclusion that in the homozygous condition the Creeper gene acts as a lethal early in embryonic development.

Since then we have accumulated a considerable amount of breeding data which will be presented in this report. Later communications will deal with the histology of the bones of Creeper fowls, the growth of the bones, the appearance of homozygous embryos, and other problems.

The material for our genetic experiments consisted of four unrelated strains of Creeper fowls. Our first Creeper line was derived from the specimens which we obtained through the kindness of Dr I. E. Cutler. The original birds were bred *inter se* and also to Leghorn pullets. To all these birds we shall refer as "American" Creepers (Plate XVI, figs. 2 and 3). Our second Creeper line descended from ten birds imported from Germany[1]; they were bred *inter se* as well as to Leghorns. To these animals we shall refer as "German" Creepers (Plate XVI, figs. 4 and 5). The third group of Creepers consisted of so-called Scotch Dumpies imported from Scotland[2] and their progeny from *inter se* matings and crosses to Rhode Island Reds. This line we shall call "Scotch" Creepers (Plate XVI, figs. 6 and 7). Finally, we were fortunate in obtaining a Creeper rooster from the Marquesas Islands. This male was bred to Leghorn pullets, and he became the ancestor of our "Marquesan" Creeper line (Plate XVI, figs. 8 and 9).

[1] Purchased from M. L. Büttner, Lauscha, Thüringen.

[2] Purchased from James W. Brown, Rosehill, Summerston, Glasgow, Scotland.

Our genetic evidence is based upon the data collected in *inter se* matings in the various Creeper lines, in crosses of Creepers with normal fowls, and in crosses of Creepers from different geographical lines. In order to facilitate the understanding of the inheritance of the Creeper traits we shall first present the data obtained in crosses of Creepers with normals.

Our records for the segregation of the characters of Creeper and normal chickens consist in descriptions of the chicks at hatching time which were checked when the birds were adult or *post-mortem*, and in descriptions of all the embryos which had failed to hatch. In addition to opening all the unhatched eggs at the end of the incubation period, we also opened the eggs in which the embryos had died during earlier stages of development. Although Creeper and normal in general can be easily distinguished after the fourteenth day of incubation by the short legs of the Creeper, these earlier records have not been included in this report since they are few and incomplete, and since there is a possibility that an early embryo with arrested development, although genetically normal, might be mistaken for a Creeper.

Crosses of Creeper with normal.

The results of various crosses of this sort are summarised in Tables I–V. Among the American Creepers (Table I) our first cross in 1926 was made to some normal pullets derived from a rumpless mating; later crosses were to Leghorns and to Frizzles and, in 1930, American Creeper pullets were mated to a Silver Spangled Hamburgh rooster. In each of these crosses the segregation of Creepers and normals closely approaches a 1 : 1 ratio, as expected if the Creeper traits are determined by a single dominant factor. In all such crosses of American Creepers there were 494 Creepers and 489 normal chickens, while the expectation was 491·5 for each class. All Creepers were heterozygous.

TABLE I.

Crosses of American Creepers with normal.

Mating	Hatched		Dead in shell		Total	
	Creeper	Normal	Creeper	Normal	Creeper	Normal
Normal ♀♀ × Creeper ♂ (1926)	25	22	6	2	31	24
Leghorn ♀♀ × Creeper ♂ (1928)	52	56	5	5	57	61
Leghorn ♀♀ × Creeper ♂ (1929)	84	91	29	30	113	121
Frizzle ♀♀ × Creeper ♂ and reciprocal (1929)	106	117	40	26	146	143
Creeper ♀♀ × Silver Spangled Hamburgh ♂ (1930)	61	89	86	51	147	140
Total	328	375	166	114	494	489
Total expectation	351·5	351·5	140	140	491·5	491·5

TABLE II.

Crosses of German Creepers with normal.

Mating	Hatched		Dead in shell		Total	
	Creeper	Normal	Creeper	Normal	Creeper	Normal
Leghorn ♀♀ × Creeper ♂ (1929)	39	35	15	6	54	41
Leghorn ♀♀ × Creeper ♂ (1930)	139	159	80	67	219	226
Ancona ♀♀ × Creeper ♂ (1930)	107	123	153	100	260	223
Total	285	317	248	173	533	490
Total expectation	301	301	210·5	210·5	511·5	511·5

TABLE III.

Crosses of Scotch Creepers with normal.

Mating	Hatched		Dead in shell		Total	
	Creeper	Normal	Creeper	Normal	Creeper	Normal
Rhode Island Red ♀♀ × Creeper ♂ (1928)	24	33	7	5	31	38
Ancona ♀♀ × Creeper ♂ (1930)	96	168	136	85	232	253
Total	120	201	143	90	263	291
Total expectation	160·5	160·5	116·5	116·5	277	277

TABLE IV.

Crosses of Marquesan Creepers with normal.

Mating	Hatched		Dead in shell		Total	
	Creeper	Normal	Creeper	Normal	Creeper	Normal
Leghorn ♀♀ × Creeper ♂ (1927)	17	14	7	4	24	18
Creeper ♀♀ × Leghorn ♂ (1929)	22	45	17	12	39	57
Creeper ♀♀ × Silver Spangled Hamburgh ♂ (1930)	14	23	27	17	41	40
Ancona ♀♀ × Creeper ♂ (1930)	124	147	158	129	282	276
Total	177	229	209	162	386	391
Total expectation	203	203	185·5	185·5	388·5	388·5

TABLE V.

All crosses of Creepers with normal.

Mating	Hatched		Dead in shell		Total	
	Creeper	Normal	Creeper	Normal	Creeper	Normal
American	328	375	166	114	494	489
German	285	317	248	173	533	490
Scotch	120	201	143	90	263	291
Marquesan	177	229	209	162	386	391
Total	910	1122	766	539	1676	1661
Total expectation	1016	1016	652·5	652·5	1668·5	1668·5

The crosses of German Creepers (Table II) consisted in two matings of Leghorn pullets with a German Creeper rooster, and in one mating of Ancona pullets to a German Creeper cockerel. Among a total of 1023 chicks and embryos there were 533 Creepers and 490 normals, figures not seriously departing from the number of 511·5 individuals expected in each class. All Creepers were heterozygous.

Our crosses of Scotch Creepers consisted in two matings. In one of these, Rhode Island Red pullets, and in the other one Ancona pullets, were mated to Scotch Creeper males. There are records for 554 individuals of which 263 were Creepers and 291 normals, expectation being 277 for each group. All Creepers were heterozygous.

The Marquesan Creeper crosses comprised four different matings. In the first one Leghorn pullets were crossed to the original Marquesan Creeper male; the second mating consisted of Marquesan Creeper females and a Leghorn cockerel; in the third experiment Marquesan Creeper females were bred to a Silver Spangled Hamburgh rooster, and the fourth cross was made up of Ancona pullets and a Marquesan Creeper male. In all these crosses taken together we have data for 777 individuals, of which 386 were Creeper and 391 normal. This segregation agrees very well with the expectation of 388·5 in each class. All Creepers were heterozygous.

The crosses in all four lines involve 3337 individuals. Of these 1676 were Creepers and 1661 normal chickens. In crosses of individuals heterozygous for one dominant factor the expectation would be 1668·5 in each class. The actual results agree very well with the expectation. These experiments furnish definite proof that the whole complex of traits characterising the Creeper fowl is governed by a single dominant Mendelian gene. All Creepers tested in crosses to normal chickens proved to be heterozygous. Reciprocal crosses gave the same results.

Inter se matings of Creepers.

According to the results of our crosses of Creepers to normal fowls we should expect *inter se* matings of Creepers to produce homozygous and heterozygous Creepers and normal chicks in the proportions of 1 : 2 : 1, or three Creepers to one normal chicken on the average.

Among the American, German, and Scotch Creepers our experiments consisted partly of *inter se* matings of the original birds or of their progeny, and partly of matings of Creepers which had been obtained from out-crosses. We had only one *inter se* mating of Marquesan Creepers which consisted of birds derived from a cross of the original Creeper rooster to Leghorn pullets.

The results of these various matings are summarised in Tables VI–X. Matings of American Creepers *inter se* (Table VI) produced a total of 391 individuals for which we have descriptions; of these 267 were Creepers, while 124 were normal. Our matings of German Creepers *inter se* (Table VII) yielded records for 318 individuals of which 199 were Creepers and 119 normal. The matings of Scotch Creepers *inter se* (Table VIII) furnished data for 363 specimens with a segregation into 248 Creepers and 115 normals. Finally, one small mating of Marquesan Creepers *inter se* (Table IX) gave 91 records with 61 Creepers and 30 normal chickens. It is obvious that in each instance there is a rather serious departure from a normal F_2-segregation. On the other hand, the result of every one of

TABLE VI.

Inter se *matings of American Creepers.*

	Hatched		Dead in shell		Total	
Year of mating	Creeper	Normal	Creeper	Normal	Creeper	Normal
1926	7	1	2	2	9	3
1927	50	23	28	19	78	42
1930	48	22	132	57	180	79
Total	105	46	162	78	267	124
Total expectation*	100·7	50·3	160	80	260·7	130·3

* If homozygous Creepers do not appear (lethal).

TABLE VII.

Inter se *matings of German Creepers.*

	Hatched		Dead in shell		Total	
Year of mating	Creeper	Normal	Creeper	Normal	Creeper	Normal
1927	6	1	12	6	18	7
1928	57	40	5	12	62	52
1929	57	36	62	24	119	60
Total	120	77	79	42	199	119
Total expectation*	131·3	65·7	80·7	40·3	212	106

* If homozygous Creepers do not appear (lethal).

TABLE VIII.

Inter se *matings of Scotch Creepers.*

	Hatched		Dead in shell		Total	
Year of mating	Creeper	Normal	Creeper	Normal	Creeper	Normal
1928	24	18	10	1	34	19
1929	129	66	85	30	214	96
Total	153	84	95	31	248	115
Total expectation*	158	79	84	42	242	121

* If homozygous Creepers do not appear (lethal).

TABLE IX.

Inter se *mating of Marquesan Creepers.*

Year of mating	Hatched		Dead in shell		Total	
	Creeper	Normal	Creeper	Normal	Creeper	Normal
1928	34	20	27	10	61	30
Expectation* ...	36	18	24·7	12·3	60·7	30·3

* If homozygous Creepers do not appear (lethal).

TABLE X.

All inter se *matings of Creepers.*

Mating	Hatched		Dead in shell		Total	
	Creeper	Normal	Creeper	Normal	Creeper	Normal
American	105	46	162	78	267	124
German	120	77	79	42	199	119
Scotch	153	84	95	31	248	115
Marquesan	34	20	27	10	61	30
Total	412	227	363	161	775	388
Total expectation*	426	213	349·3	174·7	775·3	387·7

* If homozygous Creepers do not appear (lethal).

the different crosses shows a satisfactory agreement with the ratio of two Creeper to one normal chick, expected if the homozygous Creeper embryos do not survive. This is strikingly illustrated by a summary of all the data for our *inter se* matings (Table X). There are records of 1163 individuals in all; among these were 775 Creepers and 388 normals. If a normal segregation had taken place, the expectation would have been 872·3 Creepers and 290·7 normal chickens. The departure of the actual results from the expectation is so wide as to rule out entirely this possibility. The expectation, if the Creeper gene in homozygous condition acts as a lethal, is 775·3 Creepers and 387·7 normals. This is in perfect agreement with our actual data and justifies the conclusion that all the homozygous Creeper embryos die during development. This conclusion is strengthened further by the fact that breeding tests proved all our Creepers to be heterozygous for the Creeper characters.

Differential hatchability.

While the results of our crosses of Creepers with normal fowls agree well with those to be expected from matings between heterozygotes and recessives, and while the records of our matings of Creepers *inter se* are in full accord with the expectations if the Creeper gene acts as a lethal in the homozygous condition, there is an outstanding difference to be noted in the hatchability of Creepers and of normal chicks.

An inspection of Table V shows that there is in the crosses of every one of the four different Creeper lines by normal a deficiency of Creepers among those chicks which hatched, and an approximately corresponding surplus of Creepers among the individuals which failed to hatch. This holds true for all the individual crosses (Tables I–IV), except one mating each among the American and German Creepers, both of which involve very small numbers.

A similar situation is met with in our *inter se* matings (Table X). With the exception of the American Creepers, we find in all the experiments again a deficiency of Creepers among the hatched chicks and a surplus among those which were found dead in the shell at hatching time. These deficiencies of chicks which hatched are also found in the individual experiments (Tables VI–IX), with the exception of the American Creepers and one German Creeper mating (1927) with negligibly small numbers.

The fact that this differential hatchability is found to a similar extent in back-crosses and in *inter se* matings, and that it occurred in all strains of Creeper fowl, seems to indicate that the residual heredity is not responsible for it. The fact that this phenomenon was observed in a similar manner in different years with varying management of the incubators appears to rule out external factors as essential agencies. We are led to the conclusion, then, that the higher mortality of the heterozygous Creeper embryos at the end of the incubation period is an expression of the Creeper gene itself. Our observations concerning the histology of the long bones of Creepers show that there is a wide range of variability leading from extreme disturbances of cartilage and bone formation to an almost normal condition. Our routine observations (not verified by measurement) suggest that it is easier to distinguish Creepers from normals among the unhatched embryos than among the hatched chicks, that is, that the more extreme variants of the Creeper condition have a smaller chance to hatch than the less extreme ones. A further indication for the low viability of the most extreme grades of the heterozygous Creeper condition is seen in the occasional appearance in back-crosses, as well as in *inter se* matings, of chicks with very short legs and an extreme bending of the tibia. Such chicks, probably chiefly due to an abnormal position of the legs caused by the bending of the tibia, are unable to stand on their legs and usually die shortly after hatching. It should be emphasised, however, that among the hatched chicks the majority of Creepers in all respects appear to be as vigorous as the normal chicks.

Crosses between different Creeper lines.

In order to decide whether the same mutation is responsible for the Creeper condition in our four different lines, we have made various crosses between these lines. The results of these experiments are summarised in Table XI. In all these matings taken together we have records for 1764 individuals, of which 1197 were Creepers and 567 normals, which is in good agreement with the expectation (1176·1 and 587·9) if the homozygous Creepers are not present. The same is true for all the individual matings. In all the experiments the results depart widely from a normal segregation. This provides additional evidence for the lethal nature of the Creeper gene. It also demonstrates that the same mutation is responsible for the Creeper traits in all four lines since otherwise no lethal action should result in such crosses.

The total results of these crosses suggest a differential hatchability similar to that found in the back-crosses and in the *inter se* matings in the different lines. In several matings, involving rather large numbers, however, this does not hold true. Since these experiments represent wider crosses than either the *inter se* crosses in the different lines or the back-crosses, it is suggested that hybrid vigour is responsible for the better hatchability of the Creeper chicks in these experiments.

TABLE XI.

Crosses of Creepers from different lines.

Mating	Hatched		Dead in shell		Total	
	Creeper	Normal	Creeper	Normal	Creeper	Normal
American ♀♀ × German ♂	141	71	40	16	181	87
German ♀♀ × American ♂	37	12	53	24	90	36
American ♀♀ × Scotch ♂	319	142	87	29	406	171
Scotch ♀♀ × American ♂	35	37	44	17	79	54
Scotch ♀♀ × German ♂	124	74	53	25	177	99
German ♀♀ × Scotch ♂	63	32	84	27	147	59
American ♀♀ × Marquesan ♂	33	21	38	22	71	43
Scotch ♀♀ × Marquesan ♂	21	12	25	6	46	18
Total	773	401	424	166	1197	567
Total expectation*	782·7	391·3	393·3	196·7	1176	588

* If homozygous Creepers do not appear (lethal).

Embryonic mortality.

The conclusion derived from the results of our *inter se* matings of Creepers, that the Creeper gene in the homozygous condition acts as a lethal, should find verification by a comparison of the embryonic mortality in *inter se* matings and in crosses of Creepers with normal fowls.

TABLE XII.

Crosses of American Creepers with normals.

Mating	Fertile eggs	Actual figures: Mortality during incubation 1–6	7–16	17–22	Hatched	Phokomelic embryos	Percentage: Mortality during incubation 1–6	7–16	17–22	Hatchability	Phokomelic embryos
Normal ♀♀ × American ♂ (1926)	71	3	12	9	47	0	4·2	16·9	12·7	66·2	0
Leghorn ♀♀ × American ♂ (1928)	101	4	3	8	86	0	4	3	7·9	85·1	0
Leghorn ♀♀ × American ♂ (1929)	253	8	3	60	182	0	3·2	1·2	23·7	71·9	0
American Creeper-Frizzle ♀♀ × Leghorn ♂ (1929)	159	13	7	26	113	0	8·2	4·4	16·3	71·1	0
Leghorn ♀♀ × American Creeper-Frizzle ♂ (1929)	176	14	5	40	117	0	8	2·8	22·7	66·5	0
American ♀♀ × Silver Spangled Hamburgh ♂ (1930)	307	18	2	137	150	0	5·9	0·6	44·6	48·9	0

TABLE XIII.

Crosses of German Creepers with normals.

Mating	Fertile eggs	1–6	7–16	17–22	Hatched	Phokomelic embryos	1–6	7–16	17–22	Hatchability	Phokomelic embryos
Leghorn ♀♀ × German ♂ (1929)	138	6	2	27	103	0	4·4	1·4	19·6	74·6	0
Leghorn ♀♀ × German ♂ (1930)	519	53	21	147	298	0	10·2	4	28·3	57·4	0
Ancona ♀♀ × German ♂ (1930)	544	58	17	238	231	0	10·7	3·1	43·7	42·5	0

TABLE XIV.

Crosses of Scotch Creepers with normals.

Mating	Fertile eggs	1–6	7–16	17–22	Hatched	Phokomelic embryos	1–6	7–16	17–22	Hatchability	Phokomelic embryos
Rhode Island Red ♀♀ × Scotch ♂ (1928)	81	3	6	13	59	0	3·7	7·4	16	72·7	0
Ancona ♀♀ × Scotch ♂ (1930)	594	52	46	220	276	0	8·8	7·7	37	46·5	0

TABLE XV.

Crosses of Marquesan Creepers with normals.

Mating	Fertile eggs	1–6	7–16	17–22	Hatched	Phokomelic embryos	1–6	7–16	17–22	Hatchability	Phokomelic embryos
Creeper ♀♀ × Leghorn ♂ (1929)	157	27	14	40	76	0	17·2	8·9	25·5	48·4	0
Creeper ♀♀ × Silver Spangled Hamburgh ♂ (1930)	87	6	7	40	34	0	6·9	8	46	39·1	0
Ancona ♀♀ × Creeper ♂ (1930)	437	25	15	138	259	0	5·7	3·4	31·6	59·3	0

In all Creeper experiments the eggs were candled at frequent intervals during the incubation period. To facilitate the presentation of these records, they are condensed into three mortality periods, namely up to the sixth day, from the seventh to the sixteenth day, and from the seventeenth to the twenty-second day. The latter class also includes embryos which were found still alive upon opening the unhatched eggs on the twenty-second day of incubation.

In Tables XII–XX are presented the records of incubation for all of our Creeper matings from 1926 to 1930. The data for the crosses of each of the four Creeper lines to normals are contained in Tables XII–XV, those for the *inter se* matings in each of the four lines in Tables XVI–XIX, and the records for the matings between Creepers of different lines are given in Table XX. The relative uniformity of the incubation records during the years 1926 to 1929 in these matings as well as in other breeding experiments, indicates that during this period the incubation management was normal. During the hatching season of 1930, however, all our incubation results were much poorer, due probably to the lack of sufficient experience of a new manager of the incubators. For our general discussion we shall, therefore, rely only on the 1926–9 results, but we shall refer to the 1930 records later. Averages have been calculated for the data obtained during the period 1926 to 1929, and these are presented in Table XXI.

In the crosses of heterozygous Creepers to normal fowls the embryo mortality during the first six days varied from 4 to 17 per cent. with an average mortality of 6·9 per cent. of all fertile eggs. In *inter se* matings of Creepers of the four different lines the mortality during the corresponding period varied from 20 to 45·5 per cent. with an average of 28·5 per cent.

From the seventh to the sixteenth day of incubation the mortality of embryos was low in all experiments, with an average of 4·6 per cent. in the crosses and 4·4 per cent. in the *inter se* matings. During the last days before hatching from 8 to 25·5 per cent. of the embryos died in the out-crosses, while the *inter se* matings showed a mortality of from 12 to 44 per cent.; the average mortality during this time amounted to 19·6 per cent. in the crosses and to 26·7 per cent. in the *inter se* matings. The hatchability varied in the crosses from 48 to 88 per cent. with an average of 68·9 per cent., while in the *inter se* matings the hatchability ranged from 12 to 66 per cent. with an average of only 40·4 per cent.

The most significant difference between back-crosses and *inter se* matings is the high early embryo mortality in the latter. A study of the

TABLE XVI.

Inter se *matings of American Creepers.*

Year of mating	Fertile eggs	Actual figures: Mortality during incubation 1–6	7–16	17–22	Hatched	Phokomelic embryos	Percentage: Mortality during incubation 1–6	7–16	17–22	Hatchability	Phokomelic embryos
1926	33	15	6	4	8	0	45·5	18·2	12·1	24·2	0
1927*	103	42	2	20	39	1	40·8	1·9	19·4	37·9	0·97
1927†	105	27	8	36	34	3	25·7	7·6	34·3	32·4	2·86
1930	386	137	20	155	74	2	35·5	5·2	40·1	19·1	0·52

* Original stock.

† Females were progeny of Leghorn × Creeper cross.

TABLE XVII.

Inter se *matings of German Creepers.*

1927	59	20	6	26	7	0	33·9	10·2	44·1	11·9	0
1928	157	31	3	20	103	2	19·7	1·9	12·7	65·6	1·27
1929	321	102	17	102	100	2	31·8	5·3	31·8	31·1	0·62

TABLE XVIII.

Inter se *matings of Scotch Creepers.*

1928	72	16	3	11	42	0	22·2	4·2	15·3	58·3	0
1929	451	118	16	121	196	6	26·2	3·5	26·8	43·5	1·33

TABLE XIX.

Inter se *mating of Marquesan Creepers.*

1928	143	40	3	46	54	9	28	2·1	32·2	37·8	6·29

TABLE XX.

Crosses of Creepers from different lines.

Mating	Fertile eggs	Actual figures: Mortality during incubation 1–6	7–16	17–22	Hatched	Phokomelic embryos	Percentage: Mortality during incubation 1–6	7–16	17–22	Hatchability	Phokomelic embryos
American ♀♀ × German ♂ (1929)	386	95	12	72	207	7	24·6	3·1	18·7	53·6	1·81
German ♀♀ × American ♂ (1930)	230	78	24	79	49	4	33·9	10·4	34·3	21·3	1·74
American ♀♀ × Scotch ♂ (1929)	885	198	17	124	546	12	22·4	1·9	14	61·7	1·36
Scotch ♀♀ × American ♂ (1930)	214	71	14	59	70	0	33·2	6·5	27·6	32·7	0
Scotch ♀♀ × German ♂ (1929)	408	99	31	81	197	15	24·3	7·6	19·8	48·3	3·68
German ♀♀ × Scotch ♂ (1930)	292	74	7	116	95	7	25·3	2·4	39·7	32·5	2·4
American ♀♀ × Marquesan ♂ (1928)	35	7	1	7	20	1	20	2·9	20	57·1	2·86
American ♀♀ × Marquesan ♂ (1930)	138	47	3	43	45	0	34·1	2·2	31·2	32·6	0
Scotch ♀♀ × Marquesan ♂ (1930)	73	10	2	31	30	0	13·7	2·7	42·5	41·1	0

TABLE XXI.

Summary of incubation data 1926–9.

Mating	Fertile eggs	Actual figures: Mortality during incubation 1–6	7–16	17–22	Hatched	Phokomelic embryos	Percentage: Mortality during incubation 1–6	7–16	17–22	Hatchability	Phokomelic embryos
Creeper × normal	1136	78	52	223	783	0	6·9	4·6	19·6	68·9	0
Creeper × Creeper (same line)	1444	411	64	386	583	23	28·5	4·4	26·7	40·4	1·59
Creeper × Creeper (different lines)	1714	399	61	284	970	35	23·3	3·6	16·6	56·6	2·0

embryonic development in *inter se* matings showed that most of the excessive mortality takes place at the beginning of the fourth day of incubation. The embryos which die at this time show a striking arrest in growth and differentiation (Plate XVI, figs. 10 and 11). All experiments and observations indicate that these embryos are the homozygous Creepers.

Another very important difference between the two types of matings is the occurrence of a peculiar embryonic malformation in the *inter se* matings which never appeared in out-crosses. Embryos of this type (Plate XVI, fig. 12) strikingly resemble phokomelia of humans and other mammals. Apparently this type of malformation has not yet been observed in chicken embryos or in birds in general. Most of these embryos die during the last third of the incubation period, but a few have been found alive upon opening the unhatched eggs on the twenty-second day of incubation. None has hatched. The fact alone that such phokomelic embryos regularly, although in small numbers, appeared in *inter se* matings of all four lines of Creeper fowls while they never occurred in any of the out-crosses, would suggest that they represent homozygous Creeper embryos which survived the early lethal period. Additional proof for this conclusion is provided by the crosses between Creepers of different lines (Table XX). In these matings the percentage of phokomelic embryos is higher and the mortality during the first six days of incubation lower than in the intra-line crosses of Creepers with each other. The average frequency of phokomelic embryos in the "pure" lines amounted to 1·59 per cent., while in the crosses between lines 2 per cent. were found (Table XXI). This increase in the frequency of phokomelic embryos, however, does not appear to be determined by the combination of two Creeper genes of different origin but seems to be caused by the hybrid vigour afforded by the union of the different residual heredity of two unrelated strains. This is shown by the fact that *inter se* matings of birds belonging to one and the same line also produced a higher percentage of phokomelic embryos if the parents represented the progeny of an out-cross to an unrelated breed (Leghorn or Rhode Island Red), as compared with the frequency of the malformation in matings of the original birds. Thus, the difference in the frequency of phokomelic embryos becomes much more striking if we add the data for *inter se* matings of F_1-Creepers from Creeper-Leghorn and Creeper-Rhode Island Red crosses to those for the crosses between different lines, that is if instead of comparing the results of *inter se* matings involving the Creeper gene of only one geographical line with those in which the Creeper genes of two different lines had been combined, we

compare the data for matings among the different original stocks with those for matings of either individuals of cross-bred origin (one Leghorn or Rhode Island Red parent) or of two different lines. In this case, we find in the matings of the original stocks (American, German, and Scotch) the following distribution:

	Mortality in 1–6 day period		Phokomelic embryos		
Fertile eggs	Actual	Percentage	Actual	Percentage	Percentage of expected homozygous embryos
1196	344	28·76	11	0·92	3·2

Among the matings between Creepers of cross-bred origin, on the other hand, the situation is as follows:

	Mortality in 1–6 day period		Phokomelic embryos		
Fertile eggs	Actual	Percentage	Actual	Percentage	Percentage of expected homozygous embryos
1962	466	23·75	47	2·4	10·9

A comparison of these data shows that in the matings between Creepers of cross-bred origin the early mortality is lower and the frequency of phokomelic embryos is higher than in *inter se* matings in the original stocks (American × American, German × German, Scotch × Scotch).

Assuming that the early mortality in out-crosses of Creepers is due to causes independent of the Creeper gene, and that the same agencies, distributed at random, operate in a similar way in homozygous and heterozygous Creepers as well as in normal embryos from *inter se* Creeper matings, the number of phokomelic embryos added to the number of embryos which died during the first six days should approximately equal the sum of 75 per cent. of the mortality during the first six days in back-crosses and of 25 per cent. of the total number of fertile eggs. For the *inter se* matings in the original stocks this expectation is 29·68 per cent. as compared with the actual figure of 30·17 per cent.; in the *inter se* matings of cross-bred Creepers or of Creepers belonging to different lines the expectation is 26·15 per cent. while the actual sum is 25·32 per cent. In both cases the agreement is very close. This is taken as evidence for the conclusion that the excessive early mortality and the number of phokomelic embryos in Creeper by Creeper matings taken together account for the 25 per cent. of homozygous Creepers which are expected but do not appear in the progeny of such matings. Our observations during the hatching season of 1930 show that under unfavourable

hatching conditions a smaller percentage of homozygous Creeper embryos survives the typical lethal period and develops into embryos exhibiting phokomelia. The frequency of such embryos in crosses between different lines was only 1·16 per cent. of all fertile eggs, and in the one intra-line mating (American × American Creeper) it amounted to 0·52 per cent. The mortality during the first six days of incubation was higher than in the years with normal incubation conditions.

In our genetic discussion we have referred to extreme variants of the Creeper condition among the newly hatched chicks. Cutler had already called attention to this peculiar type of chick which he described as follows: "Some of the chicks when hatched show a peculiar outbending of the leg at the knee and hock on one side. Such specimens move about in a manner similar to a chick with a broken leg. In a few instances individual specimens show this abnormality on both sides, and they are absolutely unable to walk at all, as the body cannot be lifted from the ground." Cutler thinks that the extreme abnormality appears in *inter se* matings only: "The foregoing suggests that the 'normal' Creepers are all heterozygous, and that the extreme abnormality represents the homozygous form. Since it has not been possible to raise any of these chicks, this hypothesis has not been tested genetically." We observed fairly frequently chicks with unilateral or bilateral leg deformities of the type mentioned by Cutler. We have found equally extreme cases of such chicks, however, in back-crosses and in *inter se* matings of Creepers. This renders the assumption impossible that such chicks are homozygous Creepers. These chicks always exhibit an extreme bending of the tibia, and this bending appears to be chiefly responsible for the dislocation of the leg and the inability of the chicks to stand. These chicks, then, must be considered the extreme variants of the heterozygous Creeper condition, and their existence may be taken as a demonstration of the fundamentally pathological nature of the Creeper variation.

SUMMARY.

The Creeper breed of fowls is characterised chiefly by an extreme shortness of the long bones of the extremities, a more or less striking bending of the tibia, and the presence of a highly differentiated fibula.

Breeding experiments with four different strains of Creeper fowl, obtained from America, Germany, Scotland, and the Marquesas Islands, led to the following conclusions:

1. The Creeper traits are determined by a single dominant Mendelian gene.

2. In homozygous condition the Creeper gene is lethal.

3. The lethal nature of the homozygous Creeper condition is demonstrated: (*a*) by the fact that only heterozygous animals exist (breeding tests); (*b*) by the segregation of two Creepers to one normal in *inter se* matings of Creepers; (*c*) by the fact that approximately 25 per cent. more embryos die in *inter se* matings than in out-crosses during the first six days of incubation.

4. The characteristic lethal period is at the beginning of the fourth day of incubation.

5. Homozygous embryos, at the age of 72 hours, show a striking retardation in growth and differentiation.

6. A small percentage of homozygous embryos in *inter se* crosses of the original stocks, and, apparently due to hybrid vigour, a considerably larger number in crosses between different Creeper lines and in *inter se* crosses of F_1-Creepers from matings with normal fowls, survive the typical lethal period. Such embryos exhibit a malformation closely resembling, if not identical with, phokomelia in humans and other mammals. They usually die during the last week of incubation, but in rare instances are still alive at hatching time; they never hatch.

7. The fact that in back-crosses as well as in *inter se* matings the proportions of Creepers to normals show a deficiency of Creepers among the hatched chicks, and a surplus of Creepers among the chicks which failed to hatch, demonstrates that even the heterozygous Creeper condition has a slightly semi-lethal nature.

8. Crosses between the different Creeper lines yielded essentially the same results with regard to segregation and embryonic mortality as did intra-line crosses. This seems to demonstrate that the Creeper condition in all four lines is due to one and the same mutation.

Acknowledgments.

Our sincere thanks are due to Dr Ira Eugene Cutler, Denver, Colorado, for the foundation stock of American Creepers, to Mr Herman Milton Hubbard, Jr, Lyme, Connecticut, for the Creeper rooster which he had obtained from natives of the Marquesas Islands, and to Mrs Anna B. Landauer for her help in tabulating the data and in many other ways.

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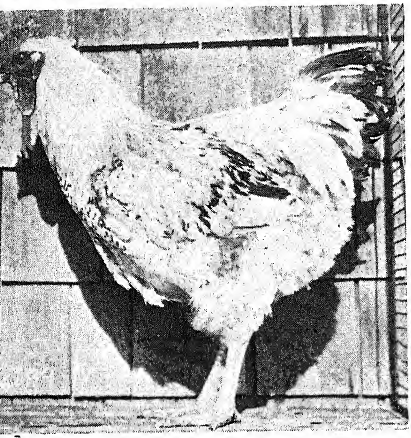

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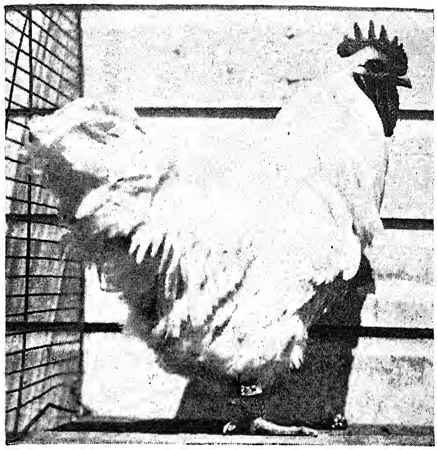

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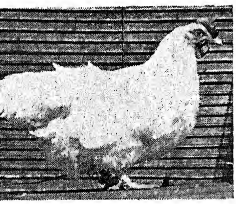

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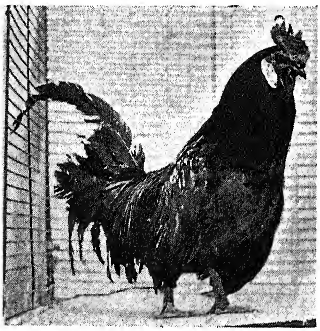

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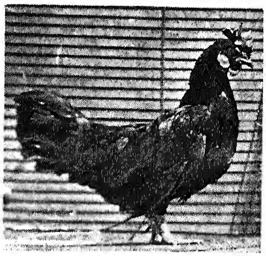

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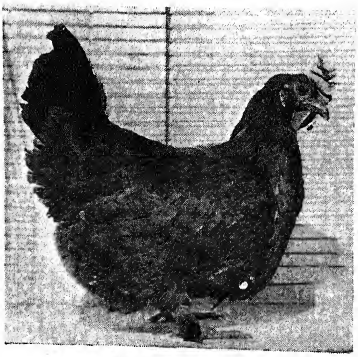

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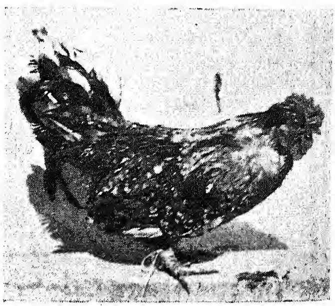

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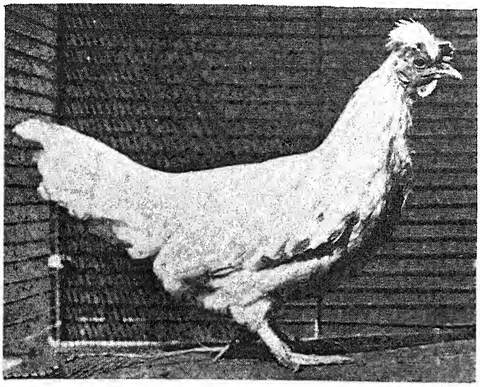

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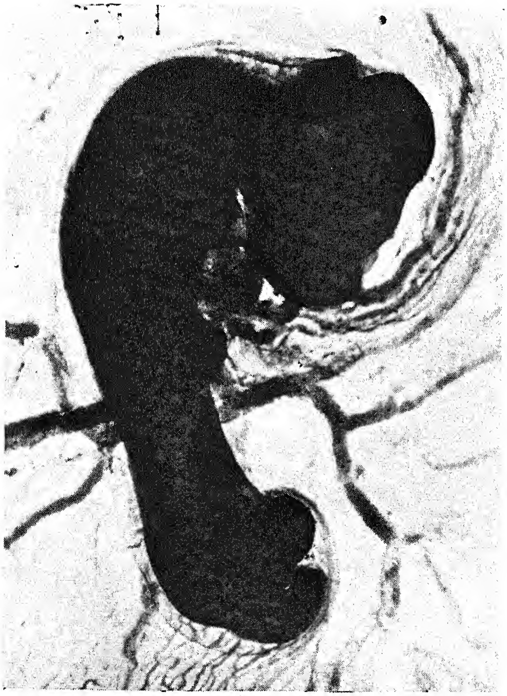

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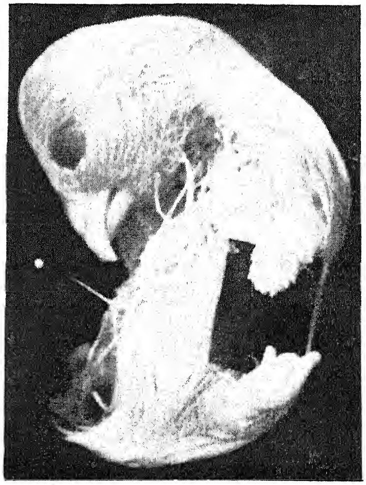

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DESCRIPTION OF PLATE XVI.

Fig. 1. Normal male for comparison with Creepers.
Fig. 2. American Creeper male.
Fig. 3. American Creeper female from an out-cross to Leghorns.
Fig. 4. German Creeper male.
Fig. 5. German Creeper female.
Fig. 6. Scotch Creeper male (Scotch Dumpie).
Fig. 7. Scotch Creeper female.
Fig. 8. Marquesan Creeper male.
Fig. 9. Marquesan Creeper female from an out-cross to Leghorns.
Fig. 10. Normal chicken embryo, 72 hours old.
Fig. 11. Homozygous Creeper embryo, 72 hours old.
Fig. 12. Homozygous Creeper embryo with phokomelia.

THE FINGER PRINTS OF TWINS.

By H. H. NEWMAN.

(*From the Hull Zoological Laboratory of the University of Chicago.*)

(With Plates XVII, XVIII.)

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I. Introduction.

The material dealt with in this paper consists of the finger prints of 100 pairs of same-sexed twins, 50 pairs diagnosed as identicals and 50 pairs as fraternals. The methods of diagnosis are described in an earlier paper (Newman, 1928). The data presented in this paper constitute an important item in diagnosis and will serve to show how, in many cases, finger patterns serve as evidence of monozygosity.

The foundations of our modern study of finger prints were laid by Galton in 1892 with the publication of his classic volume on finger prints.

As the result of this pioneer study, increased interest has been manifested in finger prints, and a great deal of detailed technical work has been done, chiefly by criminologists. For the most part these studies have dealt with the classification and cataloguing of finger prints for identification of criminals. Consequently very little has been done towards solving the biological problems involved.

One of the most important biological studies of finger prints since that of Galton was published in this *Journal* by Kristine Bonnevie (1924). Her study was based upon the finger prints of 24,518 Norwegian criminals. She discusses and gives examples of the main pattern-types and the various combinations of these. The three main pattern-types in Galton's classification, which is employed by Bonnevie, are whorls, loops and arches. The whorls have two triradii, the loops one triradius, and the arches none. Evidently the whorl is the most complete expression of digital pattern, and is usually considered to be phylogenetically the most primitive; the loop is a partially reduced whorl; while the arch is the most reduced of all, and may be considered as a vestigial pattern, though phylogenetically the most advanced.

Statistical studies of the relative frequency of the three main pattern-types were made by Bonnevie, first for the total of all fingers, and secondly according to their distribution among the five fingers. In her material 25·65 per cent. of all fingers show whorls, 66·95 per cent. loops, and 7·4 per cent. arches. The distribution of the various types of pattern on the five fingers of the two hands revealed many striking peculiarities, and these run somewhat the same for all races, although significant minor racial differences exist. Inasmuch as the present paper concerns itself largely with these matters, we shall not review all of Bonnevie's data here, but shall reserve most of them for later discussion.

Bonnevie also finds that the phenotypical character of finger patterns depends upon the interaction of three independently varying genetic factors: (1) the tendency to twist; (2) the general shape of pattern (circular or elliptical); and (3) the quantitative value as determined by the number of ridges involved in the pattern.

Thirty-one pairs of twins, all same-sexed, were studied by Bonnevie with reference to the quantitative values of the finger patterns. Fifteen of these pairs were classed as monozygotic, though the criteria for such classification were rather indefinite. These 15 pairs showed a coefficient of correlation of $+0{\cdot}924 \pm 0{\cdot}037$, a figure which, in the light of our results, suggests that a few fraternal pairs might have been included among the identicals.

Without further preliminary review of Bonnevie's monograph, we may now proceed with the presentation of our own data.

II. THE DISTRIBUTION OF FINGER PRINT PATTERN-TYPES IN OUR TWINS.

In our 100 pairs of twins taken as a whole the three main pattern-types occurred in the following percentages: whorls 34 per cent., loops 61·25 per cent., arches 4·75 per cent. Our Chicago material is seen to show a considerably higher percentage of loops and a considerably lower percentage of arches than that of Norwegian criminals as studied by Bonnevie.

In another part of her paper Bonnevie gives a table showing the statistical occurrence of pattern-types (whorls, loops and arches) in nine different races. In this table it is noteworthy that the Norwegian criminal data run the lowest of all in percentage of whorls, the highest in percentage of arches and second to highest in percentage of loops. It is not surprising then that our group of twins, taken from the environs of Chicago and derived from many races, should differ in percentages of pattern-types from the pure Norwegian group, and we might expect them to approximate very closely the average for the nine races listed in Bonnevie's table (p. 19). This expectation is actually realised. Our figures also agree closely with those of Cummins and Midlo (1927) for 100 European-Americans, which show 32·1 per cent. whorls, 62·7 per cent. loops, and 5·2 per cent. arches.

In Tables I and II (p. 418), showing the distribution of pattern-types upon the various digits of 100 identical twins and 100 fraternal twins, three types of whorls and two types of loops are listed separately, and the explanation of this will be given in the next section of the present paper. It will be noted further that the identical twins average much higher in whorls, much lower in arches, and slightly lower in loops than the fraternal twins. These differences may or may not be significant. The number of individuals, only 200 altogether, is probably not large enough to lend much statistical importance to differences of this sort. Two or three less pairs of identical twins with whorls on all fingers would very materially have lowered the percentage of whorls in the whole group, while two or three more pairs showing a preponderance of arches would have brought up the percentage of arches to that of the fraternal twins. Hence it seems fair to consider these differences between identical and fraternal twins as without statistical significance, and to lump together

TABLE I.

Distribution of pattern-types on the digits of 50 pairs of identical twins.

Type of pattern	Digits of right hand I	II	III	IV	V	Total of right	Digits of left hand I	II	III	IV	V	Total of left	Total of both
Ulnar whorls	34	19	17	29	17	116	26	18	15	31	16	106	222
Radial whorls	1	21	2	2	0	26	0	25	0	0	0	25	51
Symmetrical whorls	11	8	4	25	8	56	9	7	6	18	5	45	101
Ulnar loops	50	32	72	42	75	271	60	26	72	48	79	285	556
Radial loops	0	17	1	0	0	18	0	22	1	0	0	23	41
Arches	4	3	4	2	0	13	5	2	6	3	0	16	29
All	100	100	100	100	100	500	100	100	100	100	100	500	1000

TABLE II.

Distribution of pattern-types on the digits of 50 pairs of fraternal twins.

Type of pattern	Digits of right hand I	II	III	IV	V	Total of right	Digits of left hand I	II	III	IV	V	Total of left	Total of both
Ulnar whorls	23	15	9	26	13	86	16	14	10	28	14	82	168
Radial whorls	1	11	1	2	1	16	1	8	1	0	0	10	26
Symmetrical whorls	15	9	12	23	4	63	16	7	10	14	2	49	112
Ulnar loops	56	28	68	46	82	280	58	31	62	57	84	292	572
Radial loops	0	23	0	2	0	25	0	28	3	0	0	31	56
Arches	5	14	10	1	0	30	9	12	14	1	0	36	66
All	100	100	100	100	100	500	100	100	100	100	100	500	1000

the data from the two tables in dealing with the problem of reversed asymmetry in patterns, a problem taken up in the subsequent section.

One other item in the distribution of pattern-types deserves some attention, namely, the unequal distribution of whorls, loops and arches in the two hands, rights and lefts. In Bonnevie's data there was a distinct preponderance of whorls on the right hands (57·27 per cent. on rights, and 42·73 per cent. on lefts); a distinct preponderance of both loops and arches on left hands (52·43 per cent. of loops on lefts, and 47·57 per cent. on rights; 53·26 per cent. of arches on lefts, and 46·74 per cent. on rights). In such large numbers of individuals these differences are undoubtedly significant, and this significance is enhanced by the fact that in our own collection of twins this same relative distribution of pattern-types holds for each group, identicals and fraternals. In the 100 identical twins 53·21 per cent. of whorls occur on right and 46·79 per cent. on left hands; 51·59 per cent. of loops on left and 48·41 per cent. on right hands; 55·17 per cent. of arches on left and 44·83 per cent. on right hands. In the 100 fraternal twins 53·93 per cent. of whorls occur on right and 46·07 per cent. on left hands; 51·43 per cent. of loops on left and 48·57 per cent. on right hands; 54·54 per cent. of arches on left and 45·46 per cent. on right hands.

The difference in distribution of pattern-types in the two hands is not very great, but it is strikingly consistent and doubtless furnishes us with another example of the workings of the asymmetry mechanism. In general the right side of the body of vertebrates, as well as other groups, is the inferior side and it may be significant that there is a consistent preponderance of the most primitive patterns (whorls) on the inferior side and an equal preponderance of the most advanced patterns, especially arches, on the superior side. Here again we see another factor other than heredity or environment, an intrinsic epigenetic factor causing differences in the expression of genetically determined characters. This factor, the asymmetry mechanism, must be held responsible for part of the relatively slight differences in digital patterns between the individuals of pairs of monozygotic twins.

The conclusions reached here are further strengthened by the fact that in identical twins the total of quantitative values of ridges in patterns is definitely greater in the right hands than in the left hands. The same is equally true for the fraternal twins. Reduction in numbers of ridges in patterns means a more advanced condition phylogenetically and, once more, it is the left side that shows the more advanced condition. The figures that lead to this conclusion are given later in the section dealing with quantitative values of finger patterns (see Tables V and VI).

This asymmetry situation is in striking contrast to that found in palm patterns, in which the left hand shows the more primitive, or fully expressed condition, and the right hand the more advanced, or poorly expressed condition. A discussion of this situation appears in a very recent paper by the present writer (Newman, 1930).

(*a*) *The distribution of radial loops on the various fingers.*

Loops constitute the commonest pattern in human fingers and the great majority of these loops, in our twin material 92·08 per cent., open upon the ulnar, or little finger, side of the digit. These are called "ulnar loops" and are designated *U* in Tables III and IV. There is thus a pronounced ulnar asymmetry of the whole hand, most of the patterns turning towards the ulnar side of the hand. The remaining loops, in our material 7·92 per cent. of all loops, involving 97 finger patterns all told, are reversed loops opening on the radial side of the digit. These are called "radial loops" and are designated *R* in Tables III and IV.

Radial loops, a relatively rare finger pattern, found in less than 5 per cent. of all fingers, have a most extraordinary distribution, being almost entirely confined to digit II, the index finger, 80 out of 97 (82·47 per cent.) of such patterns being on that digit.

Bonnevie also noted and discussed the fact that, in Norwegian criminals, loops as a rule open on the ulnar side of the finger. In her collection 5·91 per cent. of all loops open on the radial side, showing a reversal of the usual asymmetry. Of the radial loops 82·57 per cent. occurred on the index finger. A reason for this is suggested by Bonnevie and discussed later.

(*b*) *The incidence of radial whorls on the various fingers.*

We also noticed an interesting phenomenon, largely overlooked by Bonnevie, namely, that whorls also show ulnar and radial asymmetry. Very frequently the whorls are twisted as a whole in a clockwise or counter-clockwise direction; or else the ridges, instead of being arranged in concentric circles, form a more or less complete spiral that, beginning on the outside and moving centralwards, turns in a clockwise or counter-clockwise direction. In prints of finger patterns of the right hand the direction of twist or spiral, as shown in prints, is typically clockwise; in those of the left hand, counter-clockwise. Thus counter-clockwise whorls on right hands and clockwise whorls on left hands are called "radial whorls," and constitute instances of reversed asymmetry belonging to the same category as "radial loops." Hence either counter-clockwise whorls in right-hand finger prints or clockwise whorls in left-hand finger prints

will be represented by the symbol *Wr*; while clockwise whorls in right-hand finger prints and counter-clockwise whorls in left-hand finger prints will be denoted by *Wu*, since they twist in an ulnar direction.

Sometimes we find a small whorl enclosed within a larger loop, the loop opening in either an ulnar or a radial direction (Plate XVII, fig. 5). Such a pattern is called a whorl, but the asymmetry of the enclosing loop must also be recorded. Thus a whorl in an ulnar loop is designated *Wlu*; one in a radial loop *Wlr*. Classified also as whorls, since they have two triradii, are double loops that are more or less spirally twisted about each other in either a clockwise or a counter-clockwise direction (Fig. 9). Such patterns are designated *Wdu* or *Wdr*, according to whether the twist is in an ulnar or a radial direction.

Of the total number of whorls 57·35 per cent. are ulnar, 11·32 per cent. are radial, and 31·32 per cent. are without definite twist or spiral, and are classified as symmetrical and designated *W*. Of the 77 radial whorls in the 100 pairs of twins, 65 (84·41 per cent.) occur on digit II. For some unknown reason radial whorls are considerably more frequent in our identical twins, while radial loops are somewhat more frequent in our fraternal twins.

The total incidence of radial loops and of radial whorls is remarkable in that 155 out of 174, or over 89·09 per cent., occur on the index finger, digit II, and the rest are scattered among the other four fingers: 3 in digit I, 9 in digit III, 6 in digit IV, and only 1 in digit V. It may also be significant that in only 1 out of 100 sets of twins does a radial loop or whorl occur on any of the other digits, except when radial loops or whorls occur on one or both the index fingers of at least one of the twins. Also there are only 3 of the 200 hands in which a radial loop or whorl occurs on digits I, III, IV or V without also occurring on digit II of the same hand. When radial patterns occur on more than one digit, the usual arrangement is that such patterns occur on digits II and III, or II and IV. In one instance (pair 43) radial whorls appear on digit II in all four hands of the twin pair, and in the right hand of twin B radial whorls occur on three digits, II, III and IV, making six radial whorls in one pair of identical twins.

The tendency towards radial patterns seems to be strongly hereditary, as it occurs on both individuals of 21 out of 50 pairs of identical twins. Even more remarkable is the fact that radial patterns occur in all four index fingers in seven pairs of identical twins.

The distribution of radial patterns in the two hands is not significantly different, 85 occurring on the right hand and 89 on the left, although in

Bonnevie's material attention is called to the fact that radial loops are commoner on the right hands.

(c) *Earlier interpretations of the mysterious distribution of radial patterns.*

The peculiar distribution of radial loops has been noted by writers previous to Bonnevie, and has been variously interpreted. Wilder (1904) seems to have been the first to call special attention to their mysterious incidence. In his monograph, "Duplicate Twins and Double Monsters," he noted "the mysterious reversal of index patterns in one hand or the other" of duplicate twins, and was inclined to consider it a consequence of twinning, a sort of vestige of asymmetry reversal belonging to the same category as *situs inversus viscerum.* "But why the transposition should affect one finger alone, or why that finger should always be the index, these are at present questions beyond solution." In his 1916 paper, "Palm and Sole Studies," he stated that in true duplicate twins one finds as a condition "not absolutely constant, but frequently noted, a reversal of the pattern of the index fingers in the two individuals, affecting either the two right hands or the two left hands, or occasionally both sets."

In *The Biology of Twins* (1917) the present writer followed Wilder in interpreting radial patterns of index fingers as evidence of mirror-imaging, or asymmetry reversal, resulting from monozygotic twinning, an interpretation that must be entirely abandoned in view of the following facts:

One need only to refer to Table II, in which the distribution of pattern-types of 50 pairs of fraternal twins is shown, to realise *that radial patterns have nothing whatever to do with monozygotic twinning.* In fact, radial patterns occur nearly as frequently in dizygotic as they do in monozygotic twins. Thus in 50 pairs of monozygotic twins 92 radial patterns occur, and in 50 pairs of dizygotic twins 82 such patterns are found.

Bonnevie also found that, in her experience, radial patterns did not occur any more frequently in twins than in other persons. It seems clear then that the occurrence of radial patterns and their concentration on index fingers cannot be explained as a result of monozygotic twinning.

Bonnevie realised this and cast about for a more satisfactory explanation. Following Wilder, Whipple, and others, she is inclined to look upon the direction of papillary ridges as playing an adaptive rôle as friction ridges. These ridges are believed to be placed "at right angles to the direction of pressure against the object to be touched." "Looking at the

human hand," she says, "we should expect to find a functional adaptation above all upon digit II, this finger being of a use more varied and extensive than any other finger....Remembering the position of the second finger when working alone in opposition to the first one (the thumb), it seems evident that the radial side of digit II and its papillary pattern should be of great importance whether the function of those lines be of a mechanical or sensory nature. Among the different pattern-types, therefore, the ulnar loop will be the one *least* useful, its ridges running away from the radial side of the finger....But no other pattern would, for the special use of the second finger, serve better than radial loops, the ridges on the radial side of the finger here being combined into pairs as arms of one and the same loop."

Apart from the fact that this type of explanation carries an unfortunate and unsupported Lamarckian implication, namely, that the direction of papillary ridges has been determined by the direction of pressures against objects and that such induced somatic modifications have become hereditary, there are other, more cogent, reasons for objecting to it.

While the argument that radial *loops* offer a better friction surface between index finger and thumb might seem to have some reasonable basis, what functional explanation can be offered for the equal prevalance of radial *whorls* on this finger? Surely no advantage could be gained by having a pattern twisted or spirally coiled counter-clockwise rather than clockwise, unless the position of the whole pattern were moved towards the radial side of the finger: and this is not usually the case.

Another crucial argument against Bonnevie's explanation of radial patterns inheres in the fact that, while radial loops are almost confined to digit II and are highly characteristic of that digit, ulnar loops, spoken of as the "least useful" pattern for that particular finger, are always more numerous than the supposedly highly advantageous radial loops. Thus there occur on the index fingers of our 100 pairs of twins 117 ulnar loops as compared with only 90 radial loops. If the advantage of radial loops be real and the effects of use inherited, why do we find more ulnar than radial loops? The direction of radial loops therefore could hardly be explained as the result of the inheritance of the effects of use unless a similar explanation be offered for that of the more numerous ulnar loops on the same digit.

(*d*) *A new interpretation of radial patterns.*

As the result of the study of a series of human hands with supernumerary fingers, and especially of double or nearly double hands, the

writer (Newman, 1923) in his book *The Physiology of Twinning* came to the conclusion that the hand is a modified symmetrical structure in which the major plane of symmetry falls between the thumb and the index finger. The hand is looked upon as a structure that has undergone asymmetrical doubling, or twinning, the first step in twinning giving rise to the thumb, on the radial side, and the primordium of the remaining digits on the ulnar side. More powerful than the mirror-image symmetry between the thumb and the rest of the hand is the deep-seated ulnar asymmetry of the whole appendage that has been shown by Harrison and others, for Amphibia, to be established prior to the visible formation of limb buds. This overpowering ulnar asymmetry nearly always determines the asymmetry of the thumb patterns. In our twin material there were no radial loops in 400 thumbs and only 3 radial whorls, indicating that the thumb is dominated by the ulnar asymmetry of the whole hand. Nearly all of the radial loops and whorls are found on the index finger, which in its origin is the twin of the thumb. Occasionally digits III and IV, along with digit II, of the same hand, assume a radial asymmetry, suggesting that at one time the primordium of the four fingers (II, III, IV, V) stood over against the thumb as its twin partner.

More commonly than not, however, the overpowering ulnar asymmetry of the whole appendage wipes out the reversed (radial) asymmetry of the fingers, acquired as the result of the first step in twinning, and imposes upon it the ulnar asymmetry of the whole hand. Evidently there is a conflict between the tendency to retain the mirror-image symmetry, resulting from the first dichotomous division of the distal portion of the limb bud, and the powerful ulnar asymmetry of the whole appendage. Sometimes, the original asymmetry prevails over most of the hand, as when two or even three fingers show reversed (radial) asymmetry of pattern; frequently, however, the reversed, or radial, asymmetry is retained only on the index finger which lies closest to the thumb; but even more commonly still, the original mirror-image asymmetry is completely obliterated by the ulnar asymmetry of the whole hand.

(*e*) *An interpretation of arches and symmetrical whorls.*

Arches do not seem at first to fit into such a scheme as that just discussed. Bonnevie, however, found arches most numerous on digit II, 44·5 per cent. of all arches occurring on this digit. Arches are also common on digit III, 29·81 per cent. of all arches appearing on that digit. In my somewhat limited collection of finger patterns the incidence of arches on digits II and III slightly favours the latter, and I find that there are only

a few less arches on digit I than on digit II. Doubtless Bonnevie's figures, since they deal with much larger numbers of cases, are more representative of the average situation than mine, and therefore may be accepted as a basis of discussion. The arch may be looked upon as either a rudimentary pattern (a pattern reduced to its lowest terms) or as a pattern produced by partial asymmetry reversal. Many arches occur in which a high, medium, or low perpendicular ridge proceeds up the centre of the pattern, resembling the centre pole of a tent. The other ridges arch over this central upright ridge as a tent roof arches over its centre pole. Such arches are appropriately called "tented arches." In my experience the arches occurring on digit II are mostly of this tented form, except in the cases of those hands in which flat arches prevail on most of the digits. As a rule, an arch occurring on a hand in which high loops or whorls prevail will be a tented arch. The prevalence of high-tented arches on digit II seems to me to signify partial reversal of asymmetry. Such a pattern may be looked upon as the resultant of a drawn battle between opposed forces; that of mirror-imaging between twin components (thumb and index finger) and that of the ulnar asymmetry of the whole appendage. Thus a tented arch may be a compromise between a radial and an ulnar loop. It seems probable also that symmetrical whorls may be a compromise between radial and ulnar asymmetrical whorls. A good many of the whorls designated *W* in my tables are slightly asymmetrical, but not very distinctly so.

The hypothesis here offered in explanation of radial patterns and their concentration on the index finger seems to the writer to approach more nearly a rationalisation of the situation than those previously presented. It agrees with, and helps to explain, the normal process of limb development, as well as the production of double or reduplicated limbs. Ordinarily, when the hand grows in its normal organic environment, its twinning tendency is more or less checked and overruled by the dominance of the body as a whole, and incipient twinning is modified by the overpowering asymmetry of position of the appendage with reference to the bodily axes. When, however, a limb bud is transplanted to a foreign position, it grows more or less independently, for a time at least, and frequently goes ahead with its twinning to the extent of producing twin limbs, each with normal digits arranged in mirror-image relation to one another. Thus a twinned, or reduplicated, limb may be thought of as a result of the physiological isolation of a limb rudiment from its organic environment, resulting in a freedom of the rudiment to complete its natural tendency to undergo twinning. In the normally developing limb

rudiment, however, the twinning process is almost completely overruled, and a hand develops as a single organ with a pronounced ulnar asymmetry, the result of its relation to the side of the body on which it grows. Only in the frequent radial patterns on the index finger do we find evidence that originally the thumb and the four fingers once held the relation to each other of twin components.

III. Comparison of finger print patterns of identical and fraternal twins.

Two different modes of comparison may be made between the two sets of twins (identical and fraternal). They may be compared with respect to the qualitative characters of their patterns, and with respect to the quantitative values of the patterns as based on a count of the number of papillary ridges involved in the pattern. For purposes of studying the qualitative resemblances and differences in the two sets of twins I have prepared the rather extensive Tables III and IV in which the type of pattern is indicated for every finger of the 200 individuals.

Key to Tables III and IV.

The following key will be necessary in the interpretation of the symbols used in the tables:

A and B (1st column)	=the two individuals of a twin pair.
M. and F. (2nd column)	=male and female respectively.
R., L., A. (3rd column)	=right-handed (R), left-handed (L. fully; l. partially), ambidextrous (A.).
+ and − (4th column)	=clockwise and counter-clockwise hair whorl, respectively.
(+ −) (4th column)	=double hair whorl, half of which is clockwise, other half counter-clockwise.
R and *U*	=single radial and ulnar loops.
W	=symmetrical whorls (Plate XVII, fig. 1).
Wu and *Wr*	=whorls with ulnar or radial twist or spiral (Plate XVII, figs. 2, 3, 4, 7, 8).
Wlu and *Wlr*	=whorls enclosed within ulnar or radial loops (Plate XVII, figs. 5, 6).
Wdu and *Wdr*	=double loops (sometimes called twin loops or lateral pocket loops) with two triradii, twisted in ulnar or radial direction (Plate XVII, fig. 9).
Ua and *Ra*	=ulnar or radial loops that are vestigial, or almost arches.
A	=arches.

In Table III the twin pairs are arranged in the order of their degrees of resemblance, the most nearly identical in all respects being first, and the least similar being last. This order is explained in an earlier paper (Newman, 1928).

An analysis of these tables leads to a number of significant conclusions. Wilder (1904) on the basis of 9 pairs of duplicate twins came to the conclusion that the palm patterns show a much higher degree of sym-

metry between right and left hands of such twins than is the case in ordinary individuals. Bonnevie studied the degree of symmetry in finger prints in connection with 15 pairs of twins adjudged by her to be monozygotic, and came to the conclusion that "the symmetry of pattern values between right and left hands of (identical) twins is not essentially different from that of single individuals."

Assuming that our 50 pairs of fraternal twins (Table IV) represent 100 single individuals, let us compare the degree of correspondence of their right and left hands (finger for finger) with that shown in identical twins (Table III).

In both sets we may consider symmetry perfect if homologous digits of the two hands of an individual correspond in type of pattern, and are therefore represented by the same symbol. In identical twins there are 17 cases with all five digits in both hands of an individual alike, 32 cases with four digits alike, 35 with three alike, 13 with two alike, and 3 alike in one digit only. In fraternal twins there are 15 individuals with all five digits alike in both hands, 34 with four alike, 38 with three alike, 8 with two alike, and 5 alike in one digit only. Thus there is no significant difference to be noted between identical and fraternal twins in the distribution of these various grades of symmetry between the hands of the same individual. If we add up the total of fingers alike in right and left hands of the same individuals, we find that there are 347 fingers alike in the two hands in identical twins as compared with 326 in fraternal twins. The difference is certainly not great, though it favours slightly the identical twins. Thus it appears that our data are rather more in accord with Wilder's statement than with Bonnevie's, though the difference is perhaps not significant.

Using the same method of comparison, we may determine whether in identical twins the resemblance between the hands of two individuals of any pair is greater or less than that between right and left sides of the same individual.

(*a*) *Comparison between hands of same individual and those of two individuals of a pair in identical twins.*

If we compare the correspondences of right hands with rights, and left hands with lefts, we find that in *identical twins* there are 27 cases in which all five fingers of the two right hands or of the two left hands are alike, 37 cases with four fingers alike, 27 with three fingers alike, 8 with two fingers alike, and 1 with only one finger alike in two left hands. This shows a same-sided (homolateral) correspondence of 351 fingers indicating a somewhat higher correspondence, in the case of identical twins,

TABLE III.

Finger print formulae of 50 *pairs of identical twins arranged in the order of their closeness of resemblance.*

No.	Sex	Handedness	Hair whorl	Finger print formulae: Digit (right hand) I	II	III	IV	V	Digit (left hand) I	II	III	IV	V
62 A	M.	R.	+	*Wu*	*Wr*	*U*	*Wu*	*Wu*	*Wu*	*R*	*Wlu*	*Wu*	*Wu*
B		R.	+	*Wu*	*Wu*	*U*	*Wu*	*Wu*	*Wu*	*Wr*	*Wu*	*Wu*	*Wu*
98 A	F.	R.	+	*U*	*U*	*U*	*U*	*U*	*U*	*R*	*U*	*U*	*U*
B		R.	+	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*
63 A	M.	R.	+	*W*	*Wr*	*Wr*	*W*	*W*	*W*	*Wr*	*Wu*	*W*	*W*
B		R.	−	*W*	*Wu*	*Wu*	*W*	*W*	*W*	*W*	*Wu*	*W*	*W*
40 A	M.	R.	(+ −)	*Wu*	*U*	*Wu*	*W*	*Wu*	*U*	*Wr*	*W*	*W*	*W*
B		R.	+	*Wu*	*U*	*U*	*W*	*Wu*	*U*	*Wr*	*U*	*W*	*Wlu*
3 A	M.	R.	?	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*
B		R.	?	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*
9 A	F.	R.	−	*U*	*U*	*U*	*U*	*U*	*Ua*	*Ua*	*U*	*U*	*U*
B		R.	+	*Ua*	*Ua*	*U*	*U*	*U*	*A*	*Ra*	*U*	*U*	*U*
80 A	F.	R.	+	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*A*	*U*	*U*
B		R.	+	*U*	*U*	*U*	*U*	*U*	*U*	*R*	*U*	*A*	*U*
67 A	M.	R.	+	*Wr*	*R*	*U*	*U*	*U*	*W*	*R*	*U*	*U*	*U*
B		l.	+	*Wu*	*Wr*	*U*	*U*	*U*	*W*	*R*	*U*	*U*	*U*
55 A	M.	R.	+	*U*	*Ua*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*
B		R.	+	*U*	*Ua*	*U*	*U*	*U*	*U*	*Ua*	*U*	*U*	*U*
35 A	M.	R.	−	*Wu*	*Wr*	*U*	*W*	*U*	*Wu*	*Wu*	*U*	*W*	*U*
B		R.	+	*Wu*	*Wr*	*W*	*W*	*U*	*Wu*	*Wu*	*U*	*U*	*U*
96 A	M.	R.	−	*Wu*	*Ra*	*U*	*U*	*U*	*Wu*	*Ua*	*Ua*	*U*	*U*
B		R.	+	*Wu*	*Ra*	*U*	*U*	*U*	*W*	*U*	*U*	*U*	*U*
73 A	F.	l.	[illegible]	*U*	*Ua*	*Ua*	*Ua*	*U*	*U*	*R*	*A*	*A*	*U*
B		A.	−	*U*	*Ua*	*A*	*A*	*U*	*U*	*R*	*A*	*A*	*U*
102 A	F.	R.	−	*W*	*W*	*U*	*W*	*W*	*U*	*W*	*U*	*W*	*Wu*
B		R.	+	*Wu*	*W*	*U*	*W*	*W*	*U*	*Wu*	*U*	*W*	*Wu*
25 A	M.	R.	−	*W*	*W*	*W*	*W*	*U*	*Wu*	*W*	*W*	*W*	*U*
B		R.	−	*W*	*W*	*W*	*W*	*U*	*W*	*W*	*W*	*W*	*U*
30 A	F.	R.	+	*U*	*A*	*U*	*U*	*U*	*U*	*R*	*W*	*Wlu*	*U*
B		R.	+	*U*	*R*	*U*	*Wlu*	*U*	*U*	*Wr*	*Wu*	*Wlu*	*U*
23 A	F.	A.	+	*U*	*Wdu*	*U*	*Wu*	*Wu*	*U*	*Wdu*	*U*	*Wu*	*U*
B		A.	+	*U*	*Wdu*	*Wu*	*U*	*Wu*	*U*	*Wdu*	*U*	*U*	*U*
94 A	F.	R.	+	*Wu*	*W*	*U*	*Wu*	*U*	*U*	*Wu*	*U*	*Wu*	*U*
B		L.	+	*U*	*Wlr*	*U*	*Wu*	*U*	*Wu*	*Wu*	*U*	*Wu*	*U*
68 A	F.	R.	−	*Wu*	*Wr*	*Wu*	*Wu*	*Wu*	*Wu*	*Wlr*	*U*	*Wu*	*U*
B		R.	+	*Wu*	*Wu*	*Wu*	*Wu*	*U*	*Wu*	*Wu*	*U*	*Wu*	*U*
49 A	F.	l.	−	*Wu*	*Wr*	*Wu*	*Wu*	*U*	*Wu*	*Wlr*	*U*	*Wu*	*U*
B		R.	+	*Wu*	*Wu*	*U*	*Wu*	*U*	*Wu*	*Wlr*	*U*	*W*	*U*
13 A	F.	R.	−	*U*	*Ua*	*U*	*U*	*U*	*U*	*R*	*U*	*U*	*U*
B		L.	+	*U*	*U*	*U*	*U*	*U*	*U*	*R*	*R*	*U*	*U*
78 A	M.	L.	+	*U*	*R*	*U*	*U*	*U*	*U*	*R*	*U*	*U*	*U*
B		R.	+	*U*	*R*	*U*	*U*	*U*	*U*	*R*	*U*	*U*	*U*
87 A	M.	A.	−	*U*	*U*	*U*	*U*	*U*	*U*	*R*	*U*	*Wu*	*Wu*
B		A.	+	*U*	*U*	*U*	*W*	*U*	*U*	*U*	*U*	*W*	*Wu*
43 A	M.	l.	−	*U*	*Wr*	*U*	*W*	*Wu*	*U*	*Wr*	*U*	*W*	*U*
B		l.	+	*U*	*Wr*	*Wr*	*Wr*	*W*	*U*	*Wr*	*U*	*W*	*U*
38 A	F.	l.	−	*U*	*U*	*U*	*Wlu*	*U*	*U*	*Wlr*	*U*	*Wlu*	*U*
B		l.	−	*U*	*U*	*U*	*Wlu*	*U*	*U*	*U*	*U*	*Wlu*	*U*

TABLE III *continued.*

No.	Sex	Handed-ness	Hair whorl	Finger print formulae: Digit (right hand) I	II	III	IV	V	Digit (left hand) I	II	III	IV	V
79 A	M.	R.	+	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*
B		L.	+	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*
72 A	M.	L.	+	*Wu*	*Wr*	*U*	*W*	*U*	*U*	*Wu*	*U*	*U*	*U*
B		R.	−	*Wu*	*R*	*U*	*W*	*U*	*U*	*Wu*	*U*	*U*	*U*
99 A	M.	R.	+	*Wu*	*R*	*U*	*U*	*U*	*U*	*U*	*U*	*Wlu*	*U*
B		R.	+	*Wu*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*	*U*
33 A	M.	L.	+	*Wu*	*Wr*	*U*	*U*	*U*	*Wu*	*Wu*	*U*	*Wu*	*U*
B		R.	+	*U*	*R*	*U*	*U*	*U*	*U*	*Wr*	*U*	*U*	*U*
53 A	M.	R.	+	*Wu*	*Wu*	*U*	*Wu*	*U*	*Wu*	*U*	*U*	*Wu*	*U*
B		L.	+	*U*	*R*	*U*	*U*	*U*	*Wu*	*Wr*	*U*	*U*	*U*
44 A	M.	L.	+	*U*	*Wlr*	*U*	*Wu*	*Wu*	*U*	*Wlr*	*U*	*U*	*U*
B		R.	+	*U*	*Wlr*	*R*	*Wu*	*U*	*U*	*Wlr*	*U*	*U*	*U*
2 A	F.	L.	?	*W*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*
B		R.	?	*W*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*
91 A	F.	R.	+	*U*	*Wu*	*U*	*U*	*U*	*U*	*U*	*U*	*Wlu*	*U*
B		R.	+	*Wu*	*U*	*U*	*U*	*U*	*U*	*Wu*	*U*	*Wlu*	*U*
100 A	M.	R.	+	*U*	*U*	*U*	*U*	*U*	*U*	*R*	*U*	*U*	*U*
B		R.	+	*U*	*R*	*U*	*Wlu*	*U*	*U*	*U*	*U*	*U*	*U*
101 A	M.	R.	+	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*W*	*Wu*	*Wu*	*Wu*
B		L.	+	*Wu*	*Wr*	*Wu*	*W*	*W*	*Wu*	*Wr*	*Wu*	*Wu*	*Wu*
70 A	M.	R.	+	*Wu*	*R*	*U*	*U*	*U*	*Wu*	*R*	*U*	*U*	*U*
B		L.	+	*Wu*	*R*	*U*	*U*	*U*	*Wu*	*R*	*U*	*U*	*U*
37 A	M.	R.	+	*U*	*U*	*U*	*U*	*U*	*A*	*Wlr*	*U*	*U*	*U*
B		l.	+	*U*	*Wlr*	*U*	*Wlr*	*U*	*A*	*Wlr*	*U*	*U*	*U*
34 A	M.	R.	+	*A*	*A*	*A*	*U*	*U*	*A*	*A*	*A*	*U*	*U*
B		l.	+	*A*	*Ua*	*Ua*	*U*	*U*	*A*	*A*	*A*	*U*	*U*
28 A	F.	R.	−	*W*	*Wlr*	*U*	*Wu*	*U*	*W*	*Wlr*	*U*	*U*	*U*
B		R.	+	*W*	*Wlr*	*U*	*Wu*	*U*	*W*	*Wlr*	*U*	*Wu*	*U*
7 A	M.	l.	−	*U*	*R*	*U*	*W*	*U*	*U*	*U*	*U*	*W*	*U*
B		l.	+	*U*	*R*	*U*	*W*	*U*	*U*	*R*	*U*	*W*	*U*
6 A	F.	R.	+	*Wu*	*U*	*U*	*W*	*U*	*Wu*	*R*	*U*	*U*	*U*
B		R.	+	*Wu*	*Wu*	*U*	*U*	*U*	*Wu*	*Wlr*	*U*	*U*	*U*
97 A	F.	R.	+	*Wu*	*Wu*	*Wu*	*Wu*	*Wu*	*U*	*U*	*Wu*	*Wu*	*Wu*
B		R.	+	*W*	*Wu*	*Wu*	*Wu*	*Wu*	*W*	*Wr*	*Wu*	*Wu*	*U*
17 A	F.	R.	+	*Wu*	*Wu*	*Wu*	*W*	*U*	*Wu*	*Wu*	*Wu*	*Wu*	*U*
B		R.	+	*Wu*	*Wu*	*Wu*	*W*	*U*	*U*	*W*	*Wu*	*Wu*	*U*
14 A	F.	R.	−	*A*	*Wlr*	*Wu*	*W*	*U*	*U*	*Wlr*	*W*	*W*	*U*
B		R.	+	*A*	*Wlr*	*Wu*	*Wu*	*U*	*U*	*Wlr*	*Wu*	*Wu*	*U*
15 A	M.	R.	+	*W*	*W*	*W*	*Wu*	*W*	*Wu*	*Wu*	*Wu*	*W*	*W*
B		R.	−	*Wu*	*Wu*	*Wu*	*W*	*W*	*Wu*	*W*	*W*	*W*	*W*
69 A	M.	R.	+	*Wu*	*Wlr*	*U*	*Wu*	*U*	*U*	*U*	*U*	*U*	*U*
B		R.	+	*Wu*	*U*	*U*	*W*	*U*	*Wu*	*U*	*U*	*U*	*U*
24 A	M.	R.	+	*U*	*Wu*	*U*	*W*	*Wu*	*U*	*Wr*	*U*	*Wu*	*Wu*
B		l.	+	*U*	*Wu*	*U*	*W*	*Wu*	*U*	*Wu*	*U*	*Wu*	*Wu*
18 A	M.	R.	+	*U*	*R*	*U*	*U*	*U*	*U*	*Wu*	*U*	*U*	*U*
B		R.	+	*U*	*W*	*U*	*Wlu*	*U*	*U*	*U*	*U*	*U*	*U*
27 A	M.	R.	−	*U*	*U*	*U*	*Wu*	*U*	*U*	*U*	*U*	*U*	*Wu*
B		l.	−	*U*	*U*	*U*	*Wu*	*Wu*	*U*	*U*	*U*	*Wu*	*Wu*
41 A	F.	L.	?	*U*	*W*	*U*	*U*	*U*	*U*	*R*	*U*	*U*	*U*
B		R.	?	*U*	*U*	*U*	*U*	*U*	*U*	*R*	*U*	*U*	*U*
60 A	F.	R.	+	*U*	*A*	*A*	*A*	*U*	*U*	*Ra*	*A*	*U*	*U*
B		l.	+	*U*	*R*	*A*	*U*	*U*	*U*	*U*	*U*	*U*	*U*

TABLE IV.

Finger print formulae of 50 pairs of fraternal twins.

No.	Sex	Handedness	Hair whorl	Finger print formulae: Digit (right hand) I	II	III	IV	V	Digit (left hand) I	II	III	IV	V
61 A	F.	R.	+	U	U	U	U	U	U	R	A	W	Wlu
B		R.	+	W	R	U	U	U	Wu	U	Ra	U	U
65 A	F.	R.	+	Wu	Wu	W	W	U	Wu	R	W	W	W
B		R.	+	W	Wr	W	W	U	W	Wr	U	W	U
74 A	F.	R.	+	Wu	Ra	U	U	U	Wu	Ra	Ra	U	U
B		R.	+	U	A	A	U	U	U	R	U	U	U
57 A	F.	R.	+	W	W	W	W	W	W	Wr	W	W	U
B		R.	−	Wu	Wu	W	W	W	Wu	Wr	W	W	Wu
39 A	M.	R.	+	W	U	U	U	U	Wu	U	U	U	U
B		R.	+	W	R	U	R	U	U	Ra	U	U	U
22 A	M.	R.	+	Wu	W	U	Wlu	U	Wu	Wlu	W	Wlu	U
B		R.	+	Wu	R	Wlu	Wlu	U	W	Wlu	U	Wlu	U
26 A	M.	R.	+	U	Wr	Wu	Wu	U	U	A	Wu	Wu	U
B		R.	+	U	Ra	U	Wlu	U	U	U	U	U	U
71 A	M.	R.	+	U	U	U	Wr	U	U	U	U	U	U
B		R.	+	U	R	U	U	U	U	R	R	U	U
86 A	M.	R.	+	W	A	A	U	U	U	Ra	A	U	U
B		R.	+	A	A	A	U	U	A	A	A	U	U
95 A	M.	R.	+	U	A	A	A	U	A	A	A	A	U
B		R.	+	U	U	U	Wu	U	U	Wu	U	Wu	U
16 A	M.	R.	+	Wu	Wlu	U	W	Wu	U	U	U	Wlu	Wlu
B		R.	+	Wu	Ua	U	Wlu	U	Wu	U	Ua	U	U
75 A	F.	R.	+	U	W	U	W	U	W	W	U	W	W
B		R.	(+ −)	U	W	U	U	U	U	Wu	U	U	U
31 A	M.	R.	+	U	Ra	U	U	U	U	R	U	U	U
B		L.	+	Wu	U	Wu	W	Wu	Wu	U	W	W	Wu
89 A	F.	R.	+	U	R	U	Wu	U	U	U	U	Wu	U
B		R.	−	U	U	U	U	U	U	Ra	Ua	U	U
45 A	F.	R.	+	U	Ua	A	U	U	U	A	A	U	Ua
B		A.	+	Ua	A	A	Ua	U	A	Ua	A	U	Ua
84 A	M.	R.	+	A	A	U	Wlu	U	A	A	U	U	U
B		R.	+	U	R	U	U	U	U	R	U	U	U
66 A	M.	R.	+	Wu	A	U	U	U	Wu	R	A	U	U
B		R.	+	U	Ua	U	U	U	U	R	U	U	U
5 A	F.	R.	+	W	W	W	W	U	W	W	W	Wu	U
B		R.	+	U	Wr	Wr	U	U	U	W	U	U	U
10 A	M.	R.	+	U	R	U	W	U	U	R	U	Wu	U
B		R.	+	Wu	Wu	Wu	Wu	Wu	W	Wu	Wu	Wu	U
50 A	F.	R.	+	U	Wlr	U	U	Wlu	U	U	U	U	W
B		R.	+	U	Wu	U	Wlu	U	U	R	U	U	U
52 A	M.	R.	+	Wu	Wr	U	W	Wu	Wu	U	U	Wu	Wu
B		R.	+	Wu	Wu	U	Wu	Wu	Wu	Wu	U	Wu	Wu
12 A	M.	L.	+	Wu	Wu	Wu	Wu	U	W	U	Wu	Wu	U
B		R.	+	Wu	Wr	Wu	Wu	Wu	W	Wr	Wu	Wu	Wu
8 A	F.	R.	+	Wu	U	U	W	Wlu	Wu	U	U	Wu	Wu
B		R.	+	U	Wu	U	Wlu	U	U	Wlr	U	U	U
85 A	F.	R.	+	U	A	U	U	U	U	R	U	U	U
B		I.	+	Wu	U	U	U	U	U	U	U	U	U
90 A	F.	R.	+	U	U	U	W	U	U	U	U	W	Wlu
B		R.	+	U	R	U	W	U	U	A	U	Wlu	U

TABLE IV *continued.*

No.	Sex	Handed-ness	Hair whorl	Finger print formulae: Digit (right hand) I	II	III	IV	V	Digit (left hand) I	II	III	IV	V
82 A	M.	R.	+	U	Ua	U	U	U	U	U	U	U	U
B		R.	+	U	A	A	U	U	U	A	A	U	U
83 A	F.	R.	+	U	U	U	U	U	U	R	A	U	U
B		l.	+	Ua	A	U	U	U	Ua	A	U	U	U
88 A	F.	R.	+	Wu	U	U	U	U	Wu	U	U	U	U
B		l.	+	Wu	W	Wlu	Wlu	U	Wu	W	W	Wu	U
81 A	M.	R.	+	U	R	U	U	U	U	R	U	U	U
B		R.	+	U	R	U	U	U	U	U	U	U	U
59 A	F.	R.	–	U	W	U	Wlu	U	U	Wu	Wlu	Wlu	U
B		R.	+	U	Wu	W	Wlu	U	U	Wu	U	Wlu	U
58 A	F.	R.	+	A	A	A	U	U	A	A	A	U	U
B		R.	+	W	W	U	U	U	W	W	A	U	U
47 A	M.	R.	+	U	U	U	W	U	U	U	U	U	U
B		R.	+	U	U	U	U	U	U	R	A	U	U
77 A	M.	R.	+	Wu	Wu	W	W	U	W	Wu	Wu	W	U
B		R.	+	U	R	U	Wlu	U	U	W	U	U	U
29 A	F.	R.	+	U	U	U	U	U	A	U	U	Ua	U
B		R.	+	U	Ua	U	R	U	U	R	U	U	U
21 A	M.	R.	+	U	Ua	U	U	U	U	R	U	U	U
B		R.	+	U	Wu	U	Wu	U	U	U	U	U	U
42 A	F.	R.	+	U	R	U	U	U	U	U	U	U	U
B		R.	+	A	A	Ua	U	Ua	A	A	Ua	U	Ua
19 A	F.	R.	+	W	W	W	W	U	W	Wr	W	W	U
B		R.	+	Wu	Wlr	U	W	Wlu	Wu	W	W	W	Wlu
93 A	F.	l.	+	W	U	U	U	U	Wu	U	U	U	U
B		R.	+	U	U	U	U	U	U	R	U	U	U
11 A	F.	R.	?	W	Wr	W	W	Wu	W	Wu	W	Wu	Wu
B		R.	?	U	U	U	W	W	U	Wu	U	W	U
36 A	F.	R.	+	W	A	U	U	U	W	R	U	U	U
B		L.	+	Wu	U	U	U	U	W	R	U	U	U
4 A	M.	L.	+	U	U	U	Wlu	U	U	Ua	U	U	Wu
B		R.	+	U	U	U	Wr	Wr	U	U	U	Wu	Wu
56 A	F.	R.	–	U	Wu	U	W	U	U	Wlr	Wlu	Wlu	U
B		R.	+	U	R	U	U	U	U	Wu	U	Wlu	U
92 A	M.	R.	+	U	R	U	Wu	Wu	U	U	U	U	U
B		L.	+	W	R	U	U	U	W	R	U	U	U
76 A	F.	R.	+	U	R	U	U	U	U	R	U	U	U
B		R.	+	U	U	U	U	U	U	U	U	U	U
32 A	M.	R.	+	U	R	U	Wlu	U	U	U	U	Wlu	U
B		R.	+	U	Wu	U	W	U	U	Wu	U	W	U
20 A	M.	R.	+	W	R	U	W	W	U	U	U	W	U
B		R.	?	Wu	Wlu	W	W	U	U	A	U	Wu	U
46 A	F.	R.	+	A	A	Wu	Wu	U	A	A	Wu	Wu	U
B		L.	+	Wu	Wu	Wu	Wu	U	U	Wu	Wu	Wu	Wu
54 A	F.	R.	+	W	Wr	U	U	U	A	R	U	U	U
B		R.	+	U	Ra	A	U	U	W	R	A	U	U
48 A	F.	R.	+	U	R	U	U	U	U	R	A	U	U
B		R.	+	U	U	A	U	U	U	U	U	U	U
64 A	F.	R.	+	Wlr	Wlr	W	Wu	Wu	Wlr	Wr	Wu	Wu	U
B		R.	+	U	Wlr	W	Wu	Wu	U	U	Wr	Wlu	U

between same (homolateral) hands of different twins than between opposite (heterolateral) hands of same twins, which was shown to involve 347 fingers.

(b) Comparison between hands of same individual and those of two individuals of a pair in fraternal twins.

In the case of *fraternal twins* there are only 2 cases of correspondence between right and right or left and left in all five fingers, 13 cases in four fingers, 42 cases in three fingers, 22 cases in two fingers, 16 cases in only one finger, and 5 cases in which all five patterns are different in the two hands. This makes a total of 248 corresponding patterns between homolateral hands of fraternal twins, over 100 less than for identical twins. This difference would be much more impressive if we were to omit from consideration in both sets of twins the patterns of digit V, which for over 80 per cent. of all human hands are ulnar loops and therefore alone account for a correspondence in over 160 fingers. If we omit digit V, we find in the other four digits 288 digits alike in homolateral hands of identical twins and 168 alike in homolateral hands of fraternal twins, a very considerable difference.

To summarise, in fraternal twins the correspondence in finger patterns between right and left hands of same individual is very much greater than between the homolateral hands of the two individuals of a pair; while in identical twins the resemblance between homolateral hands of twins is greater than that between heterolateral hands of the same individual.

A much more striking inter-individual resemblance is revealed when we compare the same hands of those twins in which homolateral resemblance is obvious, and combine with this the comparison between the right hand of one twin and the left hand of the other twin in those cases where heterolateral cross resemblance is clear, as in pairs where one twin is partially or completely left-handed or has a counter-clockwise hair whorl. The result of such a comparison gives the following figures: in 33 cases all five fingers are alike, in 38 cases four fingers are alike, in 20 cases three fingers are alike, in 9 cases two fingers are alike. There are no cases in which there are fewer than two fingers alike. The total of fingers alike is 395, as compared with 351 when homolateral hands of two individuals are rigorously compared, and with 347 when heterolateral hands of same individuals are compared. This difference would be considerably more impressive, for the reason above noted, were we to compare only the first four fingers.

These statistical results tend to support the conclusion stated in a previous paper (Newman, 1928) "that in monozygotic twins there is stronger cross resemblance between the hands of one twin and those of the other than between the two hands of the same individual." The existence of resemblances of this sort, when finger prints and palm patterns are considered together, is of the greatest value as an aid in diagnosing twins as to their monozygotic origin. The rule holds in all cases that seem in other respects unequivocally monozygotic. Consequently, when in a few slightly doubtful cases, the rule is found to hold, this goes far towards settling the diagnosis in favour of monozygotic origin.

(c) *Resemblances in finer details of pattern.*

While the codified formulae of finger print patterns shown in Tables III and IV indicate in a rough way the various degrees of resemblance between the finger prints of twins, far more convincing evidence of resemblance is afforded by a comparative study of the finer details of pattern peculiarities in homologous finger prints. The ideal way of presenting these data would be to publish half-tone enlarged reproductions of the 2000 finger prints involved, but unless this study were of extreme importance such extravagance of illustration would be unwarranted. It seems well, however, to illustrate the character of resemblance by means of a few instances that may be considered as typical (see Plate XVIII, figs. 10–16).

(d) *Never complete identity between finger prints of twins.*

In this connection the writer would like to take the opportunity of putting himself right with a number of police officials, as to the possibility that the finger prints of identical twins might cause difficulty for the finger print experts. On one occasion in a public lecture on twins we stated that frequently the individual finger prints were "extraordinarily alike." A newspaper reporter in a summary of the lecture quoted us as saying that the finger prints of twins are "often alike." The reporter, no doubt with conservative intent, omitted the word "extraordinarily." This omission, however, radically changed the meaning. "Alike" means identical or indistinguishable, while "extraordinarily alike" implies only a high degree of similarity.

The result of this publicity was that for two weeks we were besieged with communications from detective bureaus all over the country requesting that we offer proof of the statement that the finger prints of identical twins are "alike." Apparently we had appeared to challenge the infallibility of finger print science as a mode of personal identification.

Needless to say, our reply was soothing to the outraged feelings of the experts, for we had to admit that, even in identical twins, *no two finger prints of different individuals are ever exactly alike.*

There are, however, numerous instances in which the prints of two or more homologous fingers are so nearly identical as to be indistinguishable to the naked eye. When, for example, the patterns in both individuals are simple loops, having the same shape and involving the same number of ridges, it is possible only by using considerable magnification to discover differences in the branching of ridges and breaks in ridge continuity. Differences of this sort, however, are certain to be found, and afford an easy means of identification. Hence there is no likelihood that, in cases of criminal procedures, one member of a twin pair might be confused with the other because of identity of finger prints.

While resemblances are sometimes closer in those cases where the finger prints consist of simple patterns, such as loops, symmetrical whorls, or flat arches, it is of greater interest and significance to find very high degrees of resemblance between the prints of homologous fingers of two individuals when the pattern in both is complex and unusual. There are in our collection a good many cases of this sort and, because such cases have frequently been allowed to weigh heavily in our diagnoses of monozygosity, it seems worth while to illustrate this condition by means of several examples.

Plate XVIII, figs. 10–16, represent typical instances where the prints of homologous fingers of two individuals, particularly at the core of the pattern, possess more or less unique peculiarities. In all of these cases it would be no exaggeration to say that the finger print of one twin is more like that of the other twin than like that of any other finger in the entire collection of 2000 fingers. Such a finding, even with no corroborating evidence, would seem to justify the diagnosis of such a pair of twins as monozygotic. In a few instances where some slight doubt as to the monozygosity of a given pair of twins has existed prior to an examination of palm and finger patterns, the discovery of such extraordinary correspondences as those figured has clinched the diagnosis. In this connection it must be said with emphasis that no cases of resemblances so close as those shown in the illustrations were ever found in the twins diagnosed as dizygotic.

From what has just been said the reader will understand that it may readily be determined whether, for example, the pattern of the third finger of the right hand of twin A is more like that of the homologous finger of twin B than like that of his own left hand. Similarly all of the

fingers may be compared, and a judgment reached as to whether in identical twins the finger prints of homolateral hands of two individual twins are more or less similar as a whole than are those of the two hands of the same individual. Such a detailed comparison has been made for the 50 pairs of identical twins in our collection.

A summary of the results of these comparisons is given below, the numbers used being those found in Tables III and IV. When the resemblance is greatest between the right hand of one twin and the right hand of the other twin of the same pair it may be designated R. like R.; when two lefts are most alike, L. like L.; when right of one is most like left of the other, R. like L.

R. like R. and L. like L.: 62, 102, 23, 13, 72, 99, 100, 14	8 sets.
R. like R.: 80, 96, 68, 87, 38, 28, 97, 17, 24	9 sets.
L. like L.: 40, 67, 73, 49, 43, 44, 91, 37, 34, 6, 69, 41	12 sets.
R. like L.: 9, 30, 94, 53, 15, 60, 33	7 sets.
All four hands equally alike: 98, 63, 3, 35, 78, 79, 2, 101, 70	9 sets.
Three hands equally alike and one different: 55, 25, 7	3 sets.
R. and L. of same individual more alike than either hand of other twin: 27	1 set.
No decision possible: 18	1 set.

In 36 out of 50 pairs there is very positively stronger cross-resemblance between hands of twins A and B than there is resemblance between two hands of the same individual. In 9 out of the remaining 14 pairs all four hands were so nearly identical that differences were too slight to permit of judgment as to the degree of resemblance between particular hands. Such pairs must, of course, be adjudged identical twins. Where three hands are equally similar there is also very strong evidence of monozygosity, but it is not possible to decide whether inter-individual resemblances are greater or less than intra-individual resemblances. In pair 18 there was no very close resemblance of any one of the four hands with any other, making a decision very difficult.

Out of 16 pairs in which R. is like L. or in which all four hands are practically alike (a condition interpreted as partial asymmetry reversal) nine pairs of twins are characterised by having one of the individuals left-handed and four pairs by having one of the individuals counter-clockwise (reversed) in hair whorl. The majority of these show also distinct reversals in palm patterns. There is thus a high degree of correlation between reversed asymmetry (mirror imaging) in finger patterns and that in the rest of the body and in the palms. Hence the fingers as well as the palms serve as indicators of bodily asymmetry reversal.

In only one case, pair 27, was there stronger intra-individual resemblance than inter-individual resemblance. The facts that in this pair the palm prints show much stronger inter-individual resemblance, that both

twins have counter-clockwise hair whorl, and that the quantitative values of the finger prints are closely similar, outweigh the divergent evidence of the qualitative resemblances in finger patterns in diagnosing this particular pair as monozygotic twins.

It may be said in concluding this phase of the study that *not one of the* 50 *pairs of fraternal twins showed stronger or even as strong inter-individual resemblance as intra-individual resemblance in details and peculiarities of finger patterns*. This furnishes a valuable criterion in diagnosing them as dizygotic in origin.

IV. Comparison of quantitative values of finger print patterns in identical and fraternal twins.

Bonnevie has devised an improved method for comparing finger prints quantitatively. Her method consists of counting the number of papillary ridges involved in each pattern. The count includes all ridges between the triradius bounding the pattern and the core, or centre, of the pattern, not counting either of the bounding ridges. Such a study is comparable with that of counting the number of scutes in the armour bands of the armadillo, and may be used to arrive at coefficients of correlation between the two hands of each twin and between the hands of the two members of the twin pair. The ridges do not run with complete regularity, some of them being interrupted or branched. Also some patterns are so broad that the prints, even when made by rolling the fingers, do not include quite the whole pattern. In such cases one has to estimate the number of ridges not printed. With regard to ridge counting Bonnevie says: "In order to diminish the effects of such irregularities the results reached by counting the ridges are not directly used for expressing the distance between triradius and centre; but they are grouped to classes marked 0–10 and distinguished as follows":

		No. of ridges	Class
Triradii	None (arches)	—	0
,,	1–2	0	1
,,	,,	1–2	2
,,	,,	3–4	3
,,	,,	5–6	4
,,	,,	7–8	5
,,	,,	9–10	6
,,	,,	11–13	7
,,	,,	14–16	8
,,	,,	17–20	9
,,	,,	>20	10

This classification is, of course, somewhat arbitrary, but will give at least as accurate results as would direct use of all ridges counted. Two

weaknesses in Bonnevie's method have developed in the course of my own work. The first of these has to do with her method of handling whorls. In order to prevent over-valuing whorls as compared with loops, she gives a value to each side of the whorl and divides it by two. When the whorls are symmetrical this procedure is quite fair, but when there are many ridges between one triradius and the centre, and few between the other triradius and centre, the total divided by two gives a relatively small pattern value that does not do justice to the pattern as a whole. It seems to me that the difference between a whorl and a loop is a qualitative one, and that a quantitative comparison would be much closer if one counted only the ridges on the longer side of all whorls. Were there some way of counting both sides of *loops* and dividing by two, we could fairly compare this with the counts of both sides of whorls, but this is impossible because of the absence of a triradius on one side of the loops. It is logical then to count only one side of a whorl, the side having the more ridges, and this has been done in the present study. It also seems to me that Bonnevie's classification is unfair to the largest patterns, in that she gives the same value, 10, to all patterns with more than 20 ridges. In my collection there are some patterns with over 30 ridges, and these should not be valued the same as those with only 21 ridges. Hence I have used the following scale of values, in which only one triradius is used for each pattern:

No. of ridges	Value	No. of ridges	Value
0	1	17–18	10
1–2	2	19–20	11
3–4	3	21–22	12
5–6	4	23–24	13
7–8	5	25–26	14
9–10	6	27–28	15
11–12	7	29–30	16
13–14	8	31–32	17
15–16	9		

This seems to give a fairer distribution of quantitative values throughout the whole series, and is less arbitrary.

No attempt was made by Bonnevie to compare finger with finger as to their quantitative values, but the totals of values of the five fingers of each hand were taken. This compares with the method used in the armadillo (Newman, 1913), where the totals of scutes in the nine bands of armour were used for comparing the degrees of resemblance among the quadruplets. The following tables (Tables V and VI) give the values obtained for both identical and fraternal twins, right hand and left hand being given separately as well as the totals of both. The figures

represented in these tables fall short of complete accuracy, especially in one respect—in the first few cases studied the fingers were not sufficiently rolled to produce the entire pattern, as in Plate XVIII, figs, 13, 14 and 16. In most cases, however, where a strong impression of close resemblance is present in the part of the pattern recorded, they were given the same numerical value. The same treatment was accorded the dizygotic twins.

TABLE V.

Quantitative values of finger patterns of 50 *pairs of identical twins.*

No.	Right hand	Left hand	Total	No.	Right hand	Left hand	Total	No.	Right hand	Left hand	Total
62 A	44	45	89	68 A	47	36	83	70 A	47	50	97
B	46	44	90	B	47	42	89	B	41	41	82
98 A	27	32	59	49 A	47	46	93	37 A	27	26	53
B	29	27	56	B	47	46	93	B	28	24	52
63 A	52	48	100	13 A	34	37	71	34 A	12	12	24
B	52	47	99	B	37	34	71	B	19	11	30
40 A	50	52	102	78 A	37	41	78	28 A	47	49	96
B	52	50	102	B	39	39	78	B	48	49	97
3 A	37	37	74	87 A	30	36	66	7 A	42	38	80
B	40	37	77	B	37	37	74	B	40	38	78
9 A	35	28	63	43 A	60	57	117	6 A	56	53	109
B	29	35	64	B	60	56	116	B	55	57	112
80 A	28	16	44	38 A	50	44	94	97 A	48	45	93
B	25	16	41	B	48	46	94	B	48	49	97
67 A	48	44	92	79 A	19	29	48	17 A	46	47	93
B	47	45	92	B	27	21	48	B	45	52	97
55 A	21	25	46	72 A	55	56	111	14 A	34	38	72
B	21	20	41	B	57	55	112	B	38	36	74
35 A	53	56	109	99 A	30	34	64	15 A	50	54	104
B	58	55	113	B	36	34	70	B	51	52	103
96 A	41	33	74	33 A	57	60	117	69 A	41	44	85
B	37	37	74	B	58	59	117	B	37	42	79
73 A	15	12	27	53 A	44	48	92	24 A	44	46	90
B	13	12	25	B	48	48	96	B	45	43	88
102 A	53	44	97	44 A	43	43	86	18 A	57	55	112
B	55	42	97	B	40	43	83	B	56	54	110
25 A	57	53	110	2 A	56	48	104	27 A	43	45	88
B	56	58	114	B	56	50	106	B	40	34	74
30 A	31	45	76	91 A	46	39	85	41 A	38	35	73
B	41	38	79	B	36	39	75	B	39	42	81
23 A	57	53	110	100 A	23	20	43	60 A	12	11	23
B	55	51	106	B	21	22	43	B	30	26	56
94 A	48	45	93	101 A	52	57	109				
B	47	49	96	B	53	56	109				

TABLE VI.

Quantitative values of finger patterns of 50 *pairs of fraternal twins.*

No.	Right hand	Left hand	Total	No.	Right hand	Left hand	Total	No.	Right hand	Left hand	Total
61 A	24	28	52	5 A	48	51	99	21 A	40	45	85
B	38	25	63	B	34	36	70	B	53	47	100
65 A	53	54	107	10 A	44	41	85	42 A	42	39	81
B	52	60	112	B	47	52	99	B	10	6	16
74 A	44	30	74	50 A	42	40	82	19 A	50	52	102
B	27	26	53	B	49	50	99	B	57	54	111
57 A	54	56	110	52 A	56	53	109	93A	54	53	107
B	49	53	102	B	48	48	96	B	30	31	61
39 A	28	27	55	12 A	47	48	95	11 A	49	49	98
B	31	27	58	B	53	53	106	B	37	33	70
22 A	50	52	102	8 A	49	48	97	36 A	39	43	82
B	54	56	110	B	36	40	76	B	42	48	90
26 A	52	42	94	85 A	19	19	38	4 A	32	31	63
B	38	47	85	B	43	37	80	B	45	43	88
71 A	37	44	81	90 A	40	41	81	56 A	41	36	77
B	52	41	93	B	36	31	67	B	33	35	68
86 A	28	25	53	82 A	27	28	53	92 A	51	51	102
B	13	7	20	B	23	18	41	B	38	32	70
95 A	10	2	12	83 A	34	21	65	76 A	28	23	51
B	41	38	79	B	12	11	23	B	29	24	53
16 A	47	41	88	88 A	36	33	69	32 A	31	34	65
B	41	38	79	B	50	50	100	B	47	51	98
75 A	46	51	97	81 A	27	29	56	20 A	48	39	87
B	42	37	79	B	34	33	67	B	44	37	81
31 A	32	26	58	59 A	48	41	89	46 A	28	29	57
B	40	44	84	B	54	51	105	B	56	56	112
89 A	34	28	62	58 A	7	9	16	54 A	35	26	61
B	16	10	26	B	41	33	74	B	11	9	20
45 A	18	13	31	47 A	40	40	80	48 A	45	38	83
B	5	3	8	B	39	20	59	B	35	30	65
84 A	10	13	23	77 A	54	54	108	64 A	47	46	93
B	31	23	54	B	57	53	110	B	38	36	74
66 A	39	35	74	29 A	19	12	31				
B	30	31	61	B	30	32	62				

Though it requires a considerable amount of careful work on the part of an experienced statistician to arrive at the various correlations capable of being determined from the figures in the above tables, it will not take long to set them down. They are shown in Table VII.

It will be noted that the correlation between identical twins as determined by Bonnevie (+ 0·924 ± 0·037) is somewhat lower than our own correlation for 50 pairs of carefully diagnosed identical twins (+ 0·95 ± 0·01). It is, however, not in great disagreement, for the probable errors calculated for her material and mine are large enough to cover the discrepancy. It is possible, as stated before, that a few of Bonnevie's

"identical twins" are fraternals. Her figure for fraternal twins (+ 0·535 ± 0·082) is somewhat higher than ours (+ 0·46 ± 0·08), but the probable errors of both are fairly large, sufficient to cover the discrepancies. The correlation between right and left hands as determined by Bonnevie is less both for identical twins and for single individuals than ours for either identical or fraternal twins. In this case the discrepancy is so great that it is not covered by the probable error. Our figures deal with larger numbers of individuals, and we find exactly the same degree of correlation (+ 0·93 ± 0·01) between right and left hands of identical twins as between right and left of fraternal twins. This finding lends no support

TABLE VII.

Coefficients of correlation between total ridge counts of five fingers of each hand based upon figures supplied in Tables V and VI.

	Identical twins	Fraternal twins
Correlation between right and left hands of each individual	$r=0·93\pm0·01$	$0·93\pm0·01$
Correlation between right hand of A and right hand of B	$r=0·92\pm0·01$	$0·34\pm0·08$
Correlation between left hand of A and left hand of B	$r=0·93\pm0·01$	$0·50\pm0·07$
Correlation between right hand of A and left hand of B	$r=0·91\pm0·02$	$0·47\pm0·07$
Correlation between left hand of A and right hand of B	$r=0·93\pm0·01$	$0·40\pm0·08$
Correlation between totals of both hands of A and both hands of B	$r=0·95\pm0·01$	$0·46\pm0·08$

Bonnevie worked out several correlations for total finger prints of the two hands of individuals of various grades of relationship which are as follows:

Correlation between 30 pairs of unrelated individuals	$r=0·270\pm0·128$
Correlation between brothers and sisters (30 pairs)	$r=0·595\pm0·118$
Correlation between fraternal twins (16 pairs)	$r=0·535\pm0·082$
Correlation between identical twins (15 pairs)	$r=0·924\pm0·037$
Correlation between right and left hands of individual identical twins (30 individuals)	$r=0·860\pm0·027$
Correlation between right and left hands of single persons (30 individuals)	$r=0·886\pm0·039$

to the statement sometimes made (Wilder), that right and left sides of identical twins are more alike than are right and left sides of single individuals, for we may consider fraternal twins are no more than sibs born together.

It may also be noted that in identical twins the total for both hands of A and B (+ 0·95 ± 0·01) is higher than any other correlation, in fact, the highest inter-individual correlation ever determined. The highest correlation previously reported was that between twin pairs of armadillo quadruplets (pairs I and II and pairs III and IV), which are true twins formed by the fission of a single embryonic primordium. This correlation,

determined for the total numbers of scutes in the nine armour bands, was $+ 0{\cdot}9294 \pm 0{\cdot}0057$ for 112 pairs (56 sets) of males; and $+ 0{\cdot}9129 \pm 0{\cdot}0059$ for 118 pairs (59 sets) of females. This averages a little more than $+ 0{\cdot}92$, which falls several points short of being as high as that in human twins ($+ 0{\cdot}95 \pm 0{\cdot}01$).

In spite of the fact that there are several cases in which there is closer resemblance between right hand of one twin and left hand of the other, the general correlation between right and right and between left and left is very high; in one case (left and left) the same as for right and left of same individuals, in the other (right and right) a little less. If we were to correlate right with right in all sets where these are closer, and right with left in the cases where these are closer, and were to combine the two into one correlation, we should get a coefficient of correlation as high as $+ 0{\cdot}95$, which would bear out our contention that there is closer inter-individual resemblance than intra-individual resemblance among identical twins.

The most impressive feature of these correlations consists in the striking differences in the figures obtained for identical and for fraternal twins. Fraternal twins have correlations for the most part below $+ 0{\cdot}5$, the usual correlation between sibs. Why most of these correlations run somewhat below $+ 0{\cdot}5$ is not clear, but if the probable error is taken into account, there is no discrepancy with sib correlations in general. The very high correlation found for the 50 pairs of twins diagnosed as monozygotic and the very low correlation found in 50 pairs of dizygotic twins both tend strongly to corroborate our diagnoses of the two classes of twins. Were there any cases of fraternals diagnosed as identicals or identicals diagnosed as fraternals, one would hardly expect the correlation for identicals to be so high or that for fraternals so low as they actually are.

(a) *Study of individual pairs of identical twins as to quantitative resemblances.*

A closer study of Table V reveals some remarkable facts about individual sets of twins with respect to the quantitative values of their finger patterns. Twelve of the 50 pairs of identical twins have exactly the same total quantitative values of the two hands. Of these 12 pairs, 9 fall among the first 25 in the list, those most alike in features and other physical characters; while none fall in the lowest 15 in the list, those least alike physically. Eight sets show a difference of only 1 in total value between the two individuals, and 13 more show a difference of 2 or 3.

On the other hand, several pairs differ as greatly as do the average of fraternal twins. Pair 60, for example, the last in the list from the standpoint of general resemblance, has a difference of 33 in total friction ridge values; pair 70 (fifteenth from the end of the list) shows a difference of 15 in ridge values; pair 91 (eighteenth from the bottom of the list) shows a difference of 10 in ridge values; and pair 27 (third from the bottom of the list) shows a difference of 13 in ridge values. When these cases are scrutinised the following facts come to light: in pair 60 the difference is found to be due to the presence of arches, with a value of 0, in digits II and IV of twin A, as against fairly high-valued loops in these fingers of twin B. The other digits are strikingly similar in the two twins. It seems probable that the difference here is a qualitative one, involving the presence of a primitive pattern in these two fingers in one twin and its suppression in the other twin. The same sort of thing is common in palm patterns in the case of identical twins, as when a thenar pattern is present in both palms of one twin and absent in one or both palms of the other. In this case the suppression of a pattern in two fingers of each hand in one pair of twins produces ten times as great a difference in total quantitative values as the average of all the other pairs of identical twins combined.

In pair 70 nearly the whole lack of correspondence is the result of a marked difference in one finger on each hand, the index finger, the radial loops of A being large, with values of 9 and 10, while those of B are small, with values of 3 each. All other fingers are strikingly similar both qualitatively and quantitatively.

In pair 91, the two left hands have exactly the same values, 39, but there is a difference of 10 in total values in the two right hands. Here again most of the difference occurs in one digit, V, in which the pattern is highly developed in A and reduced to a vestige in B.

In pair 27 there is a most striking resemblance in the details of patterns between the right hand of A and the left hand of B, the only marked difference being in digit III, A having an extensive loop with twelve ridges and B a vestigial loop with but one ridge.

The total difference between A's and B's of 50 pairs of identical twins is 182, of which about one-third (61) is contributed by the four pairs just discussed. In each of these cases the difference seems to be due to a suppression of a pattern in one or two fingers, rather than to purely quantitative differences in pattern values.

(b) Resemblances in total quantitative values of the right and left hands in identical twins.

As was done in the case of pattern-types, it is possible to list the 50 pairs of identical twins according to the closeness of resemblance of right and left hands in their total ridge values. The following list gives the data:

R. like R. and L. like L.: 63, 80, 67, 102, 23, 49, 43, 38, 33, 2, 100, 101, 18	13 sets.
R. like R.: 55, 94, 68, 6, 97, 24, 41	7 sets.
L. like L.: 73, 99, 91, 28, 7	5 sets.
R. like L.: 62, 98, 40, 9, 35, 25, 13, 79, 72, 14, 69, 30	12 sets.
Three hands alike and one different: 3, 44, 53	3 sets.
R. and L. of same twin more alike than like either hand of opposite twin: 96, 78, 87, 70, 34, 27, 60	7 sets.
No decision possible: 37, 17, 15	3 sets.

Only 7 pairs of twins depart from the rule that inter-individual resemblance is stronger than intra-individual resemblance in one or both twins. In four of these cases, as has been explained, the discrepancy is due to the suppression of one or two patterns rather than differences in quantitative values. It should be noted that 25 pairs show homolateral resemblance and 12 pairs heterolateral resemblance between twins.

V. Comparison between armadillo quadruplets and human twins with respect to integumentary structures.

In comparing armadillo quadruplets with human twins it will be well to consider quadruplets as double twin pairs and to compare twin pairs of armadillo to twin pairs of man. Our comparison will concern itself with the question whether in the case of asymmetrical peculiarities, such as double bands and scutes, the right side is more often like the right (or left like left) than right is like left; and whether homolateral resemblance is greater or less than heterolateral.

With respect to band anomalies we may list the following cases (Newman, 1913):

Set K 87	In foetuses	I and II	R. like R. and L. like L.
		III and IV	R. like L.
Set K 30	,,	I and II	L. like L.
Set K 4	,,	I and II	L. like L.
Set C 1	,,	I and II	R. like R.
		III and IV	R. like L.
Set C 29	,,	III and IV	L. like L.
Set C 40	,,	I and II	R. like L.
Set C 101	,,	III and IV	R. like R., also R. like L.
Set K 2	,,	I and II III and IV	3 alike and 1 different.
Set A 64	,,	III and IV	R. like R. and L. like L.
Set A 96	,,	I and II	R. like R.
		III and IV	R. like R.
Set K 80	,,	I and II	L. like L.
		III and IV	R. like L.

Here there are twelve cases of homolateral resemblance and five cases of heterolateral resemblance, or mirror-imaging. In fact, homolateral resemblance is about twice as frequent as heterolateral in both armadillo quadruplets and human twins.

In the case of asymmetrical scute anomalies it is almost impossible to be sure whether the individual anomalies are equivalent units, for they occur singly at highly variable parts of the carapace in twin pairs. Yet even in scute anomalies homolateral resemblance is far commoner than heterolateral resemblance, there being eight cases of the former to three cases of the latter which are unequivocal. It appears then that in the armadillo as well as in man there is a preponderance of homolateral resemblance in asymmetry as compared with heterolateral, a fact which reinforces our conviction that twinning in man must be essentially the same sort of process as that known for the armadillo, and that twinning in man takes place at about the same time and is related to the symmetry and asymmetry mechanism in the same ways as in the armadillo.

VI. Summary.

1. The finger prints of 50 pairs of twins diagnosed as identical (monozygotic) and of 50 pairs diagnosed as fraternal (dizygotic) were studied and classified as to pattern-types. In general, the distribution of whorls, loops and arches is about the same in the two groups of twins and agrees with that of the general population of single individuals.

2. In both groups of twins radial (reverse) loops are largely confined to the index finger (digit II), only about 8 per cent. being distributed among the other four fingers.

3. Whorls also commonly show ulnar and radial twists and spirals. Those with radial asymmetry, as was the case in radial loops, are largely confined to the index finger. Only about 15 per cent. of the total of radial loops occur on the other four fingers.

4. This remarkable incidence of radial patterns is interpreted as being the result of an early twinning, or dichotomy, of the limb bud, giving rise to the primordia of the thumb and the remainder of the digits. Since the thumb practically always has ulnar asymmetry, the frequency of radial patterns on digit II is believed to be a vestige of a mirror-image relationship once present in the bilateral halves of a twinning appendage. As development proceeds, the position of the limb with respect to the bodily axes affects the symmetrical relations of the twin components in such a way that the whole appendage develops a strong ulnar asymmetry, and this is expressed in the patterns of most of the fingers. Only in the index

finger, the original twin part of the thumb, is the original twinning relation retained in the form of numerous radial (reversed) patterns.

5. Tented arches, so common on index fingers, are interpreted as instances of partial asymmetry reversal, such an arch being a compromise between an ulnar and a radial loop.

6. A detailed comparison of the pattern-types of identical and fraternal twins is made with respect to whether there is greater resemblance between hands of opposite twins or between opposite hands of same twins. In identical twins the rule is that one or both hands resemble the hands of the other twin more strongly than do opposite hands of same individual. Quite the reverse is true for fraternal twins. This may be used as a criterion for the diagnosis of doubtful twin pairs.

7. As the result of counting the friction ridges in the finger prints, using a method somewhat different from that of Bonnevie, it was found that in quantitative pattern values the coefficient of correlation between right and left hands of the same individual is the same for both identical and fraternal twins ($+ 0{\cdot}93 \pm 0{\cdot}01$); that for identical twins the correlation between total values of right plus left hands of A and B is $+ 0{\cdot}95 \pm 0{\cdot}01$, and only $+ 0{\cdot}46 \pm 0{\cdot}08$ for fraternal twins. The correlation between one or both hands of opposite twins is greater for identical twins than that between opposite hands of same individuals; while exactly the reverse is the case for fraternal twins.

8. Studies of individual pairs of twins are presented to show parallel resemblance, mirror-image resemblance, and lack of resemblance. These data cannot be summarised.

9. A comparison is made between the finger patterns of human twins and the band and scute patterns in armadillo quadruplets with respect to the relative frequency of parallel-imaging and mirror-imaging of asymmetrical peculiarities. In both man and the armadillo parallel-imaging is about twice as frequent as mirror-imaging. This emphasises the probability that twinning in man is closely similar in time and in method to that in the armadillo, and that there exists in both the same intimate relation between twinning and the symmetry and asymmetry mechanism.

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DESCRIPTION OF PLATES XVII, XVIII.

Plate XVII.

Figs. 1–9. Sample finger prints from right hands, showing various types of symmetrical and asymmetrical whorls. 1, a symmetrical whorl. 2, 4, 7 and 8, whorls showing the normal asymmetry, called ulnar whorls (*Wu*), and with a clockwise twist or spiral. 3 and 6, whorls showing reversed asymmetry, called radial whorls (*Wr*), and with a counter-clockwise twist or spiral. 5, a whorl within an ulnar loop (*Wlu*). 9, a double loop with a reversed or counter-clockwise twist (*Wdr*), classed as a whorl because it has two triradii. (Slightly enlarged.)

Plate XVIII.

Figs. 10–16. Examples of the closest approach to identity between the patterns of homologous fingers in three pairs of identical twins. 10 *a* and 10 *b*, for example, represent homologous patterns in two individuals of the same pair of identical twins. These examples are chosen, in spite of the fact that some of them are incomplete, because they represent the ways in which the centres or cores of patterns show close resemblances even when the pattern is unusual or unique in character. (Slightly enlarged.)


1
2
3
4
5
6
7
8
9


10a
11a
12a
10b
11b
12b
13a
13b
14 a
14 b
15 a
15 b
16 a
16 b

GENETICS AND CYTOLOGY OF THE TETRAPLOID FORM OF *PRIMULA SINENSIS*.

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(With Plates XIX–XXIV and Three Text-figures.)

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Introduction.

The study of polyploidy in its different forms has, in recent years, added largely to our knowledge and comprehension of genetical and evolutionary problems. The findings of the cytologists that, in a great many cases, closely allied species can be arranged in series of multiples of a haploid chromosome number already pointed to polyploidy as a factor in evolution. Steps towards the formation of new species are, no doubt, found in cases like *Primula Kewensis* (Newton and Pellew, 1929) and *Nicotiana* (Clausen and Goodspeed, 1925), where species crossings are followed by doubling of the chromosomes. From a genetical standpoint the multiplying of the chromosomes will, as pointed out by Morgan

(1926), offer an opportunity of increasing the numbers of new genes, and thereby enlarge the possibilities of evolution. Of more special interest to the cytologist and the geneticist is the behaviour of the chromosomes in polyploid forms, the inter-relationship between chromosomes and genes, and the opportunity they offer of studying the gene in different quantities.

The present investigation, which deals with the tetraploid forms of *Primula sinensis*, was started by the writer in 1922 at the John Innes Horticultural Institution and carried on there until 1926. It represents a continuation and extension of experiments started by the late R. P. Gregory, whose material and unpublished data were kindly handed over to me by the late Prof. W. Bateson. For the great privilege of working in his laboratory under his genial and inspiring supervision I am exceedingly thankful.

The tetraploid form of *P. sinensis* was first described genetically and cytologically in a preliminary report by the late R. P. Gregory (1914). Plants of giant growth were found to have twice as many chromosomes as the common variety of *P. sinensis*. While this latter form has 12 pairs of chromosomes in its somatic cells, the tetraploids were found to have 24 pairs. Genetic experiments proved beyond doubt that this multiplication is due to a longitudinal splitting of the chromosomes, since the doubling of the chromosomes is evidently accompanied by a corresponding doubling of genetical factors. In the somatic cells of such tetraploids, the chromosomes are present in sets of four homologous chromosomes instead of in pairs as in diploids. Consequently we get a more complicated distribution of genetical factors during maturation divisions, resulting in F_2 and back-cross ratios differing from those usually found.

The object of the present investigation has been to study in detail the different features of these tetraploid plants. Their fertility has been examined and compared with the fertility of diploids, while their cross-fertility with diploids has also been tested. Considerable stress has been laid upon settling the exact F_2 and back-cross ratios for a number of genes, and on the study of their quantitative nature through external manifestation when present in different doses. Further, it is hoped that the experiments have thrown some light upon the problems of linkage in tetraploids; to my knowledge it is the first time linkage has ever been studied in a tetraploid form. Finally, the cytological behaviour of the chromosomes during maturation divisions, especially through their diakinetic stages, has been studied as far as possible in a material which does not lend itself easily to cytological research.

Origin and appearance of tetraploid plants.

The giant variety of *P. sinensis* appears to have arisen spontaneously among diploid plants. Two of the tetraploids used in the earlier experiments were found by Gregory in his own strains of diploid plants. Others were brought in from Messrs Sutton's nurseries in the course of both his and my own experiments. Once in my own experience a new tetraploid plant appeared among a family of pure-bred diploid plants at the John Innes Horticultural Institution.

As already mentioned the doubling of the chromosomes can only be due to a longitudinal splitting of the chromosomes. There are two ways in which this is likely to happen: (1) the tetraploid condition may arise from a union of two germ cells, both of which have the unreduced diploid number of chromosomes; (2) if at one of the first divisions of the fertilised egg the chromosomes divide but fail to separate, this may lead to the formation of a tetraploid plant. Cytological observations make both methods possible. The existence of diploid gametes has been frequently demonstrated for several species, whilst at the same time the appearance of tetraploid cells in somatic tissue is a fairly common phenomenon. Gairdner (1926) describes a tetraploid form of *Campanula persicifolia*. In the diploid variety of this species she finds that diploid gametes of both sexes occur not infrequently, and suggests that the meeting of two of these gametes may have been the origin of the tetraploid form. On the other hand, diploid gametes in *P. sinensis* have never been observed, and although I am not prepared to say that they do not occur, I am confident that it is a very rare phenomenon, and that the chances for the meeting of two such gametes are very small. More likely the tetraploidy in this case, as suggested by Gates (1909) for *Oenothera*, is due to a suspended mitosis at the first or at one of the earlier divisions of the fertilised egg. There is, however, in the present case no way of distinguishing between these two methods of origin. The genetical and cytological results are in both cases alike, viz. the production of a plant with all its chromosomes in sets of four. In *P. Kewensis* (Newton and Pellew, 1929) we have a controlled case of tetraploidy having originated through doubling of chromosomes in somatic tissue. In this case one branch only of a plant had its chromosome number doubled. Clausen and Goodspeed (1925) take it that their tetraploid *Nicotiana* hybrid arose from a doubling of the chromosome number immediately or soon after fertilisation. Although both these cases deal with interspecific hybrids I think this is

no reason why their way of forming tetraploids should not be the same as in *P. sinensis*.

The tetraploid *P. sinensis* is in every respect a coarser and bigger plant than its diploid ancestor. Gregory (1909) and Keeble (1912) have shown that this larger growth is due to an increase in size of every cell of the plant. Otherwise the known varieties of tetraploids closely resemble the diploid form from which they arose, except for differences brought about by heterozygotic conditions. In this respect *P. sinensis* differs from tetraploid forms of other species. Thus in *Datura* the leaves of tetraploids are generally broader than in diploids, and the capsule is spherical instead of ovate (Blakeslee, Belling and Farnham, 1923). "Telham Beauty," the tetraploid form of *C. persicifolia*, has a much shallower corolla compared with the deep bell-shaped one of the diploid form (Gairdner, 1926). Again, in *Oenothera gigas* the pollen grains have four instead of three germ pores (Gates, 1911). In artificially produced tetraploids of *Solanum* Jörgensen (1928) describes the difference in leaf shape as distinct and constant. All these differences are supposed to arise as a direct consequence of the enlarged nuclei.

Fertility in tetraploids.

The tetraploid variety of *P. sinensis* soon proved to be less fertile than its diploid ancestor. Table I gives the total seed-setting in diploids of the year 1925 compared with the seed-setting in tetraploids of the years 1924 and 1925.

TABLE I.

Seed-setting in diploid and tetraploid P. sinensis.

	No. of flowers fertilised	Capsules				No. of seeds	
		Set	%	Failed	%	Total	Per capsule
Diploid plants, 1925	2032	1326	65·3	706	34·7	17292	13·04
Tetraploid plants, 1924 and 1925	2099	1218	58	881	42	8475	6·95

Table I reveals that in tetraploids more flowers fail to set after pollination, and that the average number of seeds per capsule is reduced to about one-half of that in diploids. In tetraploids only 58 per cent. of the pollinated flowers develop their seeds as compared with 65 per cent. in diploids, and the average amount of seeds per set capsule is about 7 against 13 in diploids.

This manner of calculating, however, gives only a rough measure of fertility. Both in diploids and tetraploids seed-setting varies considerably,

some varieties being much more fertile than others, while hybrid vigour also plays some part. Hence the fertility in a particular year, as calculated in Table I, will largely depend upon what kinds of plants have been used for breeding. One gets a truer picture of the difference between diploids and tetraploids by comparing the maximum of seeds per capsule which it is possible to get from any one plant. In Table II the plants used for breeding during the years mentioned have been arranged according to their average number of seeds per capsule.

TABLE II.

Number of seeds per capsule obtained from each plant used for breeding.

		Diploid and tetraploid plants arranged according to their average number of seeds per capsule						
		0	1–5	6–10	11–15	16–20	21–50	Total
Tetraploids 1924–5	Actual numbers	13	88	39	9	—	—	149
	Percentage	8·7	59	26·2	6·1	—	—	
Diploids 1925	Actual numbers	24	37	47	29	11	21	169
	Percentage	14·2	22	28	17·1	6·4	12·3	

The great bulk (59 per cent.) of tetraploid plants gave only from 1 to 5 seeds per capsule, while no single plant gave more than 15 seeds per capsule. In diploids, on the other hand, most of the plants used gave more than 6 seeds per capsule, while a great many plants surpassed these numbers and quite a few gave even from 40 to 50 seeds per capsule.

The question at once arose whether the lowered fertility in tetraploids was in any way connected with the heterostylism characteristic of this species. It is a well-known fact that *P. sinensis* has two kinds of flowers, short- and long-styled, this dimorphic heterostylism being determined by one single pair of genes[1]. Earlier experiments all agree that in diploid *P. sinensis* legitimate unions (short × long or *vice versa*) are the more fertile. Darwin (1880) found that legitimate crosses gave about twice as many seeds per capsule as the illegitimate crosses (long × long or short × short). Gregory (1911) found the difference somewhat smaller, and states that in his experiments long-styled plants were on the whole more fertile. The problem which here arises is whether heterostylism affects seed-setting in tetraploid plants, and if so, how.

Table III shows the result obtained from legitimate and illegitimate crosses in diploids and tetraploids respectively.

[1] Short-styled plants have the anthers at the opening of the corolla tube, while in long-styled plants the anthers are found at the bottom of the tube.

TABLE III.

Seed-setting from legitimate and illegitimate crosses of tetraploid plants of the years 1925 and 1926 and diploid plants of the year 1925.

		No. of flowers fertilised	No. of capsules with seed	No. of seeds	No. of seeds per capsule
Legitimate crosses					
Short × long	Tetraploid	179	155 (86·6 %)	2336	15·1
	Diploid	35	31 (88·6 %)	529	17
Long × short	Tetraploid	111	63 (56·8 %)	535	8·5
	Diploid	89	59 (66·2 %)	426	7·7
Illegitimate crosses					
Short × short	Tetraploid	354	269 (76 %)	2087	7·8
	Diploid	266	191 (71·8 %)	2342	12·3
Long × long	Tetraploid	1401	707 (50·3 %)	3259	4·6
	Diploid	1642	1045 (63·6 %)	13995	13·4

In the diploid plants of 1925 the effect of heterostylism is hardly traceable. The legitimate union short × long gave the highest number of seeds per capsule; but, on the other hand, the reciprocal cross, long × short, gave a comparatively low average of seeds per capsule, the illegitimate unions at the same time both showing fairly good results.

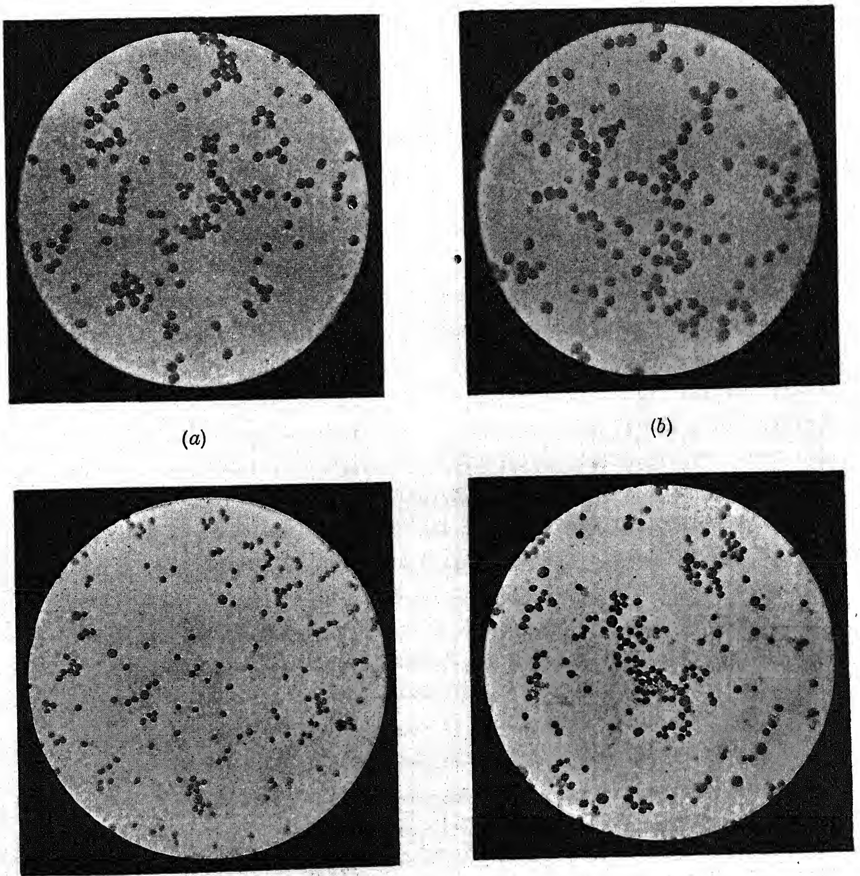
Turning to the tetraploids we meet certain peculiarities. From legitimate unions more seeds were on the whole obtained, although the difference between the legitimate cross, long × short, and the illegitimate cross, short × short, is too small to be of much significance. The legitimate crosses, short × long, gave, on the other hand, more than thrice as much seed per capsule as the illegitimate crosses, long × long, the latter showing a very low fertility. This fact is of some significance for the final result. As shown in Table III the combination, long × long, has been used far more frequently than any other cross. This is due to the coincidence that most of the varieties used in the experiments have been long-styled, and in tetraploids it takes some time to combine them all with heterostylism. Here then we have one reason why in the present experiments a distinct lowering of the average amount of seeds per capsule is found.

In the hope that more light would be thrown upon these questions of fertility, an examination of pollen grains, their development and germination power, was undertaken. The result of these rather extensive investigations was, however, disappointing in so far as these questions are concerned.

The distribution of the chromosomes during maturation divisions in pollen mother cells of tetraploid plants, and the possible significance of the phenomena here met with in connection with the problem of fertility, will be discussed in a later section. After reduction apparently regular

pollen tetrads are formed. Irregularities like those found by Gairdner (1926) in *Campanula* do not appear; for she found that in the tetraploid variety of *C. persicifolia* an abnormal distribution of chromosomes not infrequently gives rise to a varying number of cells, from three to six, inside the pollen mother cell's wall. Similar cases are described by Jörgensen (1928) in *Solanum*.

Ripe pollen of tetraploid *P. sinensis* looks relatively good, although a certain proportion of shrivelled grains is always present. Microphotographs of pollen from short- and long-styled flowers of diploids and tetraploids respectively are shown in Text-fig. 1.



(a) (b) (c) (d)

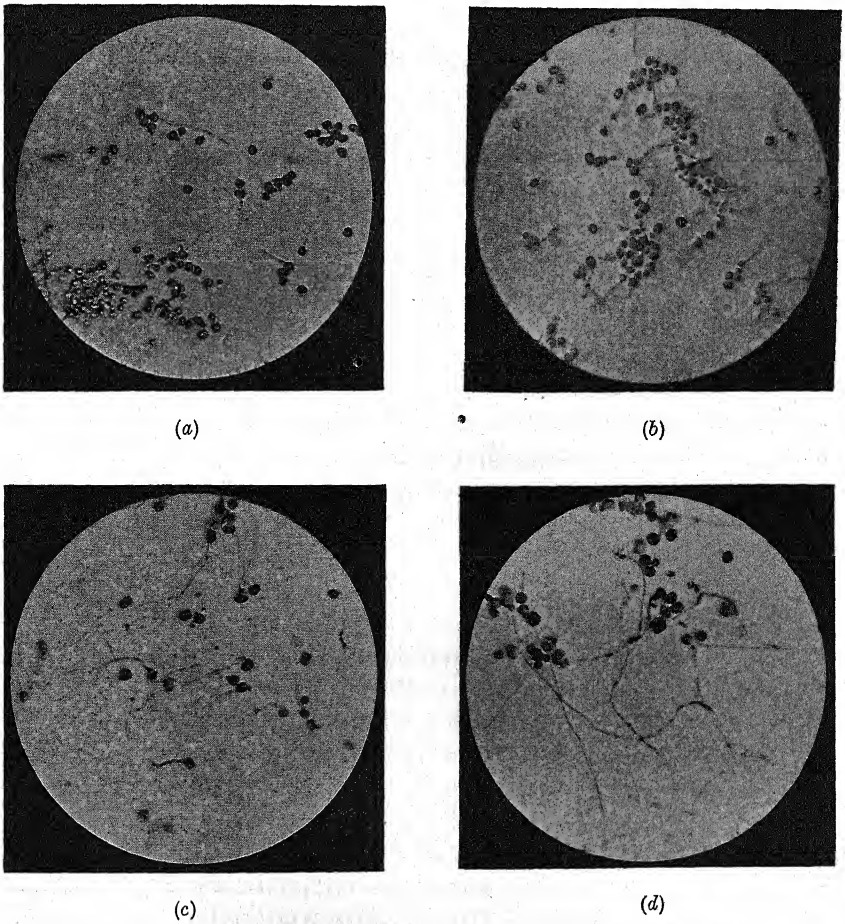
Text-fig. 1. Pollen grains from diploid and tetraploid plants: (*a*) short-styled diploid; (*b*) short-styled tetraploid; (*c*) long-styled diploid; (*d*) long-styled tetraploid.

The difference in size between pollen from diploids and tetraploids is striking. The photographs further bring out that characteristic differences, existing in diploids between pollen from short- and long-styled plants, are maintained in tetraploids. Pollen from short-styled plants of both forms consists of uniformly developed, slightly oval-shaped grains. Long-styled flowers have, on the other hand, two kinds of pollen grains, viz. a few large round thick-walled grains (diameter in tetraploids measuring about 42μ), together with a quantity of smaller more oval grains (the longer axis measuring in tetraploids about 28μ). The photographs further show that, whereas diploid anthers contain very few bad grains, a certain amount of bad pollen is present in tetraploids, and considerably more bad shrivelled pollen grains in long-styled than in short-styled flowers. A rough count gave for long-styled tetraploid plants 5 per cent. larger, mostly round, pollen, 55 per cent. ordinary sized oval pollen grains, and 40 per cent. shrivelled pollen. Short-styled plants, on the other hand, were found to have 70 per cent. good pollen, 8 per cent. of smaller grains, and only 22 per cent. bad shrivelled grains.

The peculiar differences between normal pollen from long-styled plants can hardly be of any significance to the problem of fertility; for similar differences in diploids have no visible effect upon the fertility of the plants. Moreover, in tetraploids, long-styled flowers fertilised by the regular pollen from short-styled plants gave less seed than the short-styled plants fertilised by the more irregular pollen from long-styled flowers. On the other hand, the presence of bad pollen indicates a lowered fertility, but it is doubtful whether the amount of shrivelled grains in itself is sufficiently large to influence the seed-setting process. There are more shrivelled grains in long- than in short-styled flowers, and yet, as already mentioned, short-styled flowers fertilised by pollen from long-styled flowers proved to be the better seed-setters.

Pollen grains of both kinds were next made to germinate on a sugar solution in agar (1 per cent.). In both cases germination started readily and almost at once on a solution containing 10–12 per cent. cane sugar. Pollen from short-styled flowers proved to germinate somewhat better than pollen from long-styled flowers, the percentages of germination being 42 and 30 respectively. Pollen from short-styled plants grew very long, healthy looking tubes, which lasted for several days on the nutrition medium (see Text-fig. 2 (*c*) and (*d*)). Only about 1 per cent. of the smaller grains started germination, and grains which did not germinate within a few hours never germinated at all. Pollen from long-styled plants had strikingly weaker tubes which, after a day or two, invariably burst at

the outer ends (see Text-fig. 2 (*a*) and (*b*)). These facts are given without any attempt to explain their cause or significance. The solution of the problem lies with the physiologists. Apart from the considerably higher percentage of germination the same differences are found in diploids. Presumably some sort of physiological difference between the stigmas of



Text-fig. 2. (*a*) and (*b*). Pollen from long-styled tetraploids. (*c*) and (*d*). Pollen from short-styled tetraploids.

short- and long-styled flowers counterbalances this difference between the two kinds of pollen, and makes the tubes grow normally down the pistil.

Summing up, these observations on the pollen and its germination proved that in tetraploid plants a certain amount of bad pollen exists,

while at the same time the power of germination is considerably lowered, both factors acting in the same direction in reducing the fertility of the plants.

A superficial examination of ovaries revealed no such occurrence of bad ovules; but this may be of no significance, since chromosomal disturbances may not assert themselves till after fertilisation.

Finally, a few words concerning seed-germination in giants. Only good-looking seeds were sown, all others being discarded. With this restriction germination was found to be only slightly lower than that of diploids. Seed from short- and long-styled plants germinated equally well, regardless of whether they originated from legitimate or illegitimate crosses. The percentage of germination was about 75.

Intersterility of tetraploids and diploids.

The difficulty of crossing tetraploids and diploids was recognised by Gregory (1914), who remarks that "up to the present time neither the *GG* nor the *GT* races of giants have given any fertile seed in crosses with various non-giant diploid races, whichever way the crosses were made." During the five years I have had the opportunity of working with *P. sinensis*, more than a hundred crossings of this kind were tried each year, but with very poor result. The first three years these attempts were entirely futile. In 1925, however, one seed was obtained from the cross tetraploid female by diploid male. This seed germinated and developed into a strong, healthy looking plant (Plate XIX), which from root-tip counts proved to have the triploid number (36) of chromosomes. The following year, 1926, two more triploid plants resulted, also from crosses, tetraploid × diploid.

Although several other varieties were tried, triploid plants have so far only been obtained when the tetraploid variety "moss-curl" was used as female parent.

Triploid plants so far have proved to be completely self-sterile. Triploid × diploid have, however, given one plant with 25 chromosomes, and tetraploid × triploid likewise one plant, which was found to have 47 chromosomes, both cases being counted from root tips by Miss Gairdner. As expected, the number of chromosomes in triploid germ cells is variable. It is noteworthy that, so far, every time any seed has resulted from crosses of this kind, plants of higher chromosome number have acted as female parents, the few successful crosses being tetraploid × diploid, tetraploid × triploid and triploid × diploid; reciprocal crosses never gave any seed capable of germinating. Miss Gairdner (1926) reports that crosses between

C. persicifolia and its tetraploid variety, "Telham Beauty," only succeeded when the latter was used as mother plant. In this case, however, the triploid offspring were self-fertile; also viable seeds were obtained from crosses triploid × tetraploid and diploid × triploid. A parallel case is reported in *Datura*, where Blakeslee, Belling and Farnham (1923) found that diploid × tetraploid gave a total of 212 failures and no successes, while the reciprocal cross, tetraploid × diploid, occasionally gave viable offspring. The phenomenon calls for a closer and more extensive examination.

GENETICS OF TETRAPLOIDS.

The tetraploid form of *P. sinensis* has in its somatic cells 12 chromosomal sets, each containing four homologous chromosomes. Hence in a homozygous plant any gene **A** will be represented four times. Heterozygous plants may, as pointed out by Gregory (1914), be any one of three possible kinds, $\mathbf{A}_3\mathbf{a}_1$, $\mathbf{A}_2\mathbf{a}_2$ or $\mathbf{A}_1\mathbf{a}_3$.

In heterozygotes of the kind $\mathbf{A}_3\mathbf{a}_1$, two types of gametes, **AA** and **Aa**, are formed in equal numbers, and since both gametes will contain at least one dose of the dominant gene, it follows that pure recessives can never be obtained from these plants either by selfing or by back-crossing. In the next generation, however, there is a chance that a few recessives may be produced from plants of the genotype $\mathbf{A}_2\mathbf{a}_2$.

The second type of heterozygote ($\mathbf{A}_2\mathbf{a}_2$) has a special interest in connection with the problems of tetraploidy. Three kinds of gametes, **AA**, **Aa** and **aa**, are here possible. As regards the relative proportion between these classes of gametes two alternatives have to be considered:

(1) Gregory (1914) assumed that in plants of the constitution $\mathbf{A}_2\mathbf{a}_2$ gametes were formed in the ratio 1**AA** : 2**Aa** : 1**aa**. Selfing these plants then would lead to a segregation of 15 dominants to 1 recessive, while from back-crossing a 3 : 1 ratio would result. The numbers he obtained from his experiments he regarded as being in fair agreement to these expectations.

(2) Shortly afterwards Muller (1914) advanced the theory that gametes must be formed in the proportion of 1**AA** : 4**Aa** : 1**aa**, giving rise to a 35 : 1 ratio from selfing and a 5 : 1 ratio from back-crossing. The numbers published by Gregory he thought to be in better agreement with this hypothesis. The data given by Gregory are, however, as Muller was well aware, hardly sufficient for settling this question. Later, Blakeslee, Belling and Farnham (1923) found in tetraploid *Datura* a strong support for the latter theory.

The problem raised is one of vital importance, inasmuch as the whole

question will depend upon the behaviour of the chromosomes during maturation divisions. If pairing takes place only between chromosomes coming from opposite parents, selfing and back-crossing F_1 plants will give the ratios proposed by Gregory. Assuming that $\mathbf{AA_1}$ came from one parent and $\mathbf{aa_1}$ from the other, the gametes obviously will be formed according to the scheme:

$$\begin{tikzcd} \mathbf{A} \arrow[r] \arrow[dr] & \mathbf{A_1} \arrow[dl] \\ \mathbf{a} \arrow[r] & \mathbf{a_1} \end{tikzcd}$$

i.e. $\mathbf{1AA} : \mathbf{2Aa} : \mathbf{1aa}$, as assumed by Gregory.

If, on the other hand, pairing takes place at random between any two of the four homologous chromosomes, regardless of whether they were derived from the same or from opposite parents, the gametes would be formed according to the following scheme:

$$\begin{tikzcd} \mathbf{A} \arrow[r] \arrow[d] \arrow[dr] & \mathbf{A_1} \arrow[d] \arrow[dl] \\ \mathbf{a} \arrow[r] & \mathbf{a_1} \end{tikzcd}$$

i.e. $\mathbf{1AA} : \mathbf{4Aa} : \mathbf{1aa}$, as first proposed by Muller (1914).

Between these two alternatives lies of course a series of intermediate possibilities based upon the alternatives that conjugation can take place between any two of the four chromosomes with unequal frequency. Pairing may, for instance, take place preferably between chromosomes coming from opposite parents.

It might seem that the better way of deciding between these alternatives would be to use $\mathbf{A_2a_2}$ plants in which one **A** and one **a** were derived from the one parent and the other **A** and **a** from the other parent. Pairing between chromosomes from opposite parents would, in this case, give nothing but **Aa** gametes, and no segregation of recessives could take place. Pairing at random would, on the other hand, lead to the same result as before. The objection to this procedure is the difficulty of getting plants made up in this way. The only method would be to cross $\mathbf{A_1a_3}$ plants; one-fourth of the offspring then should have the constitution wanted. The testing of these plants is, however, a laborious and uncertain affair owing to the small number of offspring obtained from any one plant.

As will be shown later, the study of certain constellations of genes exhibiting linkage phenomena provides another method of judging between these alternatives.

The third class of heterozygotes, plants of the genotype $\mathbf{A_1a_3}$, will behave like diploids, giving the ordinary Mendelian ratios of 3 : 1 by selfing and 1 : 1 by back-crossing.

In diploid *P. sinensis* a great many genes are known, and their mode of inheritance has been extensively studied (Gregory, 1911; Gregory, de Winton and Bateson, 1923). Fortunately tetraploid plants have appeared within several varieties of diploids containing different genes, and we are able to study the behaviour of these identical genes in fourfold condition. In the following account seven different genes, their way of manifestation and their mode of inheritance in tetraploid plants, will be described. In the tables given, numbers from the year 1922 and onwards are from my own experiments, while numbers from earlier dates represent unpublished results from Gregory's note-books.

Heterostylism. (S–s.)

The characteristics of heterostylism have already been described (p. 451 note). For brevity, therefore, it is sufficient to use the terms short- and long-style, the position of anthers being always closely related to the development of the style.

The complete dominance of the gene for short-style is in diploids a well-established fact. In tetraploids we find that all three kinds of heterozygotes are phenotypically alike and like the homozygous dominant, one dose of **S** being sufficient to produce the whole effect of short-styledness. The character was used by Gregory (1914); the numbers given in his report are small, but, though differently interpreted by him, in close agreement with what follows.

Table IV gives the result of back-crossing 11 plants of the type $\mathbf{S_2s_2}$. The constitutions of these plants are known only through their offspring, owing to the difficulty of establishing a pure dominant strain. The tetraploid mutant came in a diploid family heterozygous for short-style, and it demands many years of breeding to make sure of a pure dominant out of this combination; one may recall that heterozygotes of the type $\mathbf{S_3s_1}$ do not give any recessives till the second generation, and then only from one-fourth of their offspring. There can, however, be no doubt of the constitution of the plants tested in the table.

The expectations for both alternatives are given. The result goes strongly against the supposition of a pairing only between chromosomes coming from opposite parents. Random assortment of the chromosomes fits, on the other hand, fairly well, although there is a lack of pure recessives.

TABLE IV.

Short-style–long-style.

S_2s_2 back-crossed.

Family	No. of plants tested	Short	Long
126–24	2	55	12
127–24	2	49	9
130–24	1	45	5
161–24	1	11	2
234–25	2	40	8
155–26	3	87	9
Total	11	287	45
Expected on a 3 : 1 ratio		249	83
		$M=7{\cdot}9$	Dev./$M=4{\cdot}8$
Expected on a 5 : 1 ratio		276·7	55·3
		$M=6{\cdot}8$	Dev./$M=1{\cdot}5$

$$M = \text{standard error} = \sqrt{\frac{p\,(n-p)}{n}}.$$

Tables V and VI, with nearly 3500 plants, demonstrate beautifully the ordinary Mendelian segregation exhibited by heterozygotes of the S_1s_3 type.

TABLE V.

Short-style–long-style.

S_1s_3 selfed.

Family	No. of plants tested	Short	Long
55–14	2	105	45
56–14	2	86	31
93–14	1	42	17
94–14	1	38	10
104–14	3	102	32
62–15	1	27	8
79–15	1	21	8
115–23	1	26	9
105–23	1	30	4
102–23	1	24	9
100–23	1	18	3
129–24	1	15	9
114–24	3	60	28
150–25	4	259	79
238–26	1	16	9
237–26	1	51	11
307–26	1	8	1
306–26	1	48	20
152–26	1	24	9
Total	28	1000	342
Expected		1006·5	335·5
		$M=15{\cdot}9$	Dev./$M=0{\cdot}4$

TABLE VI.

Short-style–long-style.

S_1s_3 back-crossed.

Family	No. of plants tested	Short	Long
56–14	1	17	27
137–15	3	44	35
43–21	1	45	33
144–22	1	32	35
141–22	1	11	7
105–23	1	8	18
103–23	1	41	36
105–23	1	20	21
102–23	4	83	108
115–23	1	51	65
114–24	3	118	88
116–24	1	20	12
129–24	2	43	50
130–24	1	14	15
165–24	1	53	50
173–24	1	28	27
170–24	1	14	15
150–25	4	131	124
152–26	2	124	113
153–26	1	17	20
156–26	4	93	96
Total	36	1007	995
Expected		1001	1001
		$M=22{\cdot}4$	Dev./$M=0{\cdot}3$

Green and red stigma. (**G**–**g**.)

G acts as a partial suppressor of colour, making not only the stigma but the whole of the pistil green. It also gives the flower colour a lighter shade. In diploids it shows complete dominance, two doses of **g** being necessary to make the pistil red and to give the flowers a darker shade. In tetraploids also only the pure recessives, $\mathbf{g}_4$, show the red colour, all three types of heterozygote having green-coloured stigma. In plants of the constitution $\mathbf{G}_1\mathbf{g}_3$, however, the flowers have a darker shade, in some cases nearly as dark as that of the pure recessive form.

Tables VII and VIII give the result of selfing and back-crossing $\mathbf{G}_2\mathbf{g}_2$ plants. In this case every plant tested came from crossing pure dominant

TABLE VII.

Green stigma–red stigma.

$\mathbf{G}_2\mathbf{g}_2$ selfed.

Family	No. of plants tested	Green	Red
55–14	2	142	6
56–14	4	186	6
104–14	3	131	3
85–15	2	31	—
182–21	1	8	—
102–23	1	32	1
105–23	1	32	2
114–24	4	128	2
116–24	1	8	—
144–25	4	250	3
145–25	1	50	1
150–25	4	326	12
152–25	2	19	1
154–25	2	20	2
155–25	3	195	6
306–26	2	92	7
307–26	1	9	—
Total	38	1659	52
Expected on a 15 : 1 ratio		1604	107
		$M=7\cdot0$	Dev./$M=7\cdot9$
Expected on a 35 : 1 ratio		1663·5	47·5
		$M=6\cdot9$	Dev./$M=0\cdot7$

TABLE VIII.

Green stigma–red stigma.

$\mathbf{G}_2\mathbf{g}_2$ back-crossed.

Family	No. of plants tested	Green	Red
56–14	1	31	12
182–21	1	16	5
102–23	4	166	26
103–23	1	66	11
105–23	1	57	11
131–23	1	14	2
114–24	4	189	42
116–24	1	28	4
144–25	4	64	10
145–25	1	18	3
154–25	2	5	—
150–25	4	210	44
155–25	3	105	25
152–26	2	206	28
Total	30	1175	223
Expected on a 3 : 1 ratio		1048·5	349·5
		$M=16\cdot2$	Dev./$M=7\cdot8$
Expected on a 5 : 1 ratio		1165	233
		$M=13\cdot6$	Dev./$M=0\cdot7$

$\mathbf{G}_4$ with pure recessives ($\mathbf{g}_4$); their genotypical constitution, therefore, being a certainty. The reason for this is that plants pure for **G** have always been available, tetraploid mutants having appeared repeatedly within diploid families pure for green stigma.

In both cases comparatively large numbers of plants are involved, and their distribution between the two classes can only be explained in one way: the chromosomes carrying **G** pair at random regardless of their origin from the same or from opposite parents. The first alternative,

pairing only between chromosomes from opposite parents, may be completely disregarded, the deviation from the expected numbers being almost eight times the standard error. Neither is there any sign of an alternative intermediate between the two.

Heterozygotes of the type $\mathbf{G_1g_3}$ give, as seen in Tables IX and X, the ordinary Mendelian type of segregation.

TABLE IX.

Green stigma–red stigma.

$\mathbf{G_1g_3}$ selfed.

Family	No. of plants tested	Green	Red
95–15	1	33	7
98–15	3	97	41
138–22	1	7	2
112–23	1	5	3
113–23	1	4	2
100–23	1	18	3
161–24	1	8	1
Total	9	172	59
Expected		173·2	57·8

$M=6{\cdot}6$ Dev./$M=0{\cdot}4$

TABLE X.

Green stigma–red stigma.

$\mathbf{G_1g_3}$ back-crossed.

Family	No. of plants tested	Green	Red
95–15	1	7	8
56–16	1	17	18
137–16	1	19	18
140–18	1	13	17
86–19	1	17	17
138–22	1	2	2
127–24	1	20	11
137–24	1	4	4
170–24	1	2	2
153–26	1	20	17
155–26	1	8	14
156–26	4	111	84
Total	15	240	212
Expected		226	226

$M=10{\cdot}3$ Dev./$M=1{\cdot}3$

Magenta and red flowers. (B–b.)

Magenta-coloured petals in *Primula* were shown by Gregory, de Winton and Bateson (1923) to be due to the interaction of two genes **B** and **R**, both possessing the property of keeping the anthocyanin in solution, and making its colour respectively blue or red. **B** working together with **R** makes the petals magenta. The combinations **Br** and **br** were found to be responsible for blue and slaty colours respectively, slaty having bluish flowers with anthocyanin present in solid form. These two last-mentioned shades, blue and slaty, have so far not appeared among tetraploids. We are here, then, only concerned with **B** and **b**, all the plants in question being homozygous in **R**.

The two colours, magenta and red, are easily distinguishable in diploids, magenta being the dominant colour. In tetraploids the classification of F_2's and back-crosses for magenta and red is less easy, because the class $\mathbf{B_1b_3}$ exhibits colours varying from magenta to almost pure red. With some practice I found it, however, possible to pick out the pure reds.

The cross, homozygous magenta × red, gives in F_1 plants of the genotype $\mathbf{B_2b_2}$ showing a full magenta colour. Selfing and back-crossing these plants (see Tables XI and XII) strikingly confirm the theory of an independent assortment of the chromosomes carrying the gene **B**. A calculation of the numbers expected on selective pairing of the chromosomes has in this case not been undertaken, firstly because of the close agreement to the second alternative, and secondly because **B** is carried by the same chromosomes as **S** and **G**, both of which, in their genetic behaviour, show independent assortment of the chromosomes in question.

TABLE XI.

Magenta–red.

$\mathbf{B_2b_2}$ selfed.

Family	No. of plants tested	Magenta	Red
98–15	2	129	4
114–24	2	61	1
152–25	1	15	—
Total	5	205	5
Expected on a 35 : 1 basis		204·2	5·8

$M=2{\cdot}4$ Dev./$M=0{\cdot}3$

TABLE XII.

Magenta–red.

$\mathbf{B_2b_2}$ back-crossed.

Family	No. of plants tested	Magenta	Red
114–24	2	115	16
126–24	1	70	18
230–25	1	11	3
155–25	3	76	11
Total	7	272	48
Expected on a 5 : 1 basis		266·6	53·4

$M=6{\cdot}7$ Dev./$M=0{\cdot}8$

The expected segregation in a 3 : 1 and a 1 : 1 ratio respectively from $\mathbf{B_1b_3}$ plants is shown in Tables XIII and XIV.

TABLE XIII.

Magenta–red.

$\mathbf{B_1b_3}$ selfed.

Family	No. of plants tested	Magenta	Red
55–14	1	88	25
56–14	1	75	31
104–14	1	59	10
114–24	1	18	8
116–24	1	7	1
115–24	1	17	4
Total	6	264	79
Expected on a 3 : 1 basis		257	86

$M=8{\cdot}0$ Dev./$M=0{\cdot}9$

TABLE XIV.

Magenta–red.

$\mathbf{B_1b_3}$ back-crossed.

Family	No. of plants tested	Magenta	Red
56–14	1	15	29
85–15	1	10	8
56–16	1	18	18
137–16	5	27	26
86–19	1	10	10
114–24	1	40	36
116–24	1	14	18
126–24	1	27	27
127–24	2	41	29
161–24	1	7	13
230–25	1	17	11
231–25	1	6	5
152–26	2	125	106
153–26	1	19	18
156–26	5	80	95
Total	25	456	449
Expected on a 1 : 1 basis		453·5	453·5

$M=14{\cdot}9$ Dev./$M=0{\cdot}2$

Dominant white. (W–w.)

In *P. sinensis* two kinds of whites are known, one due to a recessive, the other to a dominant gene. Only the last one has so far been found in the tetraploid variety.

W acts as an inhibitor, preventing the development of colour in the corolla, the effect being stronger in the peripheral parts of the petals. Pure white flowers can only be produced in connection with green stigma (**G**). Dominant whites with red stigma (**g**) possess a dark flush round the corolla tube, a type of flower known as "Duchess." The dominance of **W** is incomplete, heterozygotes with green stigmas mostly showing a faint tinge of colour; with red stigma the depth of this tinge is considerably intensified. The effect of **W** is also, to some degree, dependent upon temperature, a lower temperature tending to deepen the colouring, while at a higher temperature heterozygotes as well as homozygotes show no trace of colour. This phenomenon is probably what is cited in every text-book on genetics as illustrating the influence of environment upon the phenotypical expression of a gene.

In tetraploids the manifestation of **W** is of a still more complex nature owing to the increased number of possible combinations between **W** and **G** and their allelomorphs. These different genotypes may, according to their colouring, be arranged in an almost continuous series, ranging from pure white through lighter and darker shades to pure magenta or red.

The following gives a list of the different phenotypes encountered in F_2's and back-crosses together with their genotypical constitution:

Green stigma ($\mathbf{G}_4$, $\mathbf{G}_3\mathbf{g}_1$, $\mathbf{G}_2\mathbf{g}_2$ or $\mathbf{G}_1\mathbf{g}_3$).

(1) *Pure white.* $\mathbf{W}_4$ or $\mathbf{W}_3\mathbf{w}_1$, in both cases together with at least two doses of **G**.

(2) *Tinged white.* Flowers faintly tinged with colour. Genotype either $\mathbf{W}_2\mathbf{w}_2$ in connection with two or more doses of **G**, or $\mathbf{W}_4$ and $\mathbf{W}_3\mathbf{w}_1$, in plants with three doses of **g**.

Plants having the constitution $\mathbf{G}_1\mathbf{g}_3\mathbf{W}_2\mathbf{w}_2$ show a darker tinge almost overlapping the next class.

(3) *Lavenders.* These shades are all due to one dose of **W** ($\mathbf{W}_1\mathbf{w}_3$), mostly together with two or more doses of **G**. They fall into two classes, magenta lavender and red or pink lavender, depending upon whether **W** partially inhibits a magenta or a red ground colour (see Plate XX, figs. 4 and 6). The intensity of the colours is extremely variable; in lighter variants it is difficult to separate magentas and reds.

Three doses of red stigma in $\mathbf{W_1w_3}$ plants give darker shades approaching a full colouring.

Red stigma ($\mathbf{g_4}$).

(4) *Duchess*. Flowers of the type described above having a dark flush round the opening of the corolla tube. Genotype $\mathbf{W_4}$ or possibly $\mathbf{W_3w_1}$. It may be mentioned that, so far, I have never succeeded in obtaining a genuine "Duchess" among tetraploids.

(5) *Tinged white on a red stigma*. In flowers of the constitution $\mathbf{W_2w_2g_4}$, the outer part of the petals is tinged, while the inner part has the flush characteristic of red stigma (see Plate XX, fig. 5).

(6) *Lavender on a red stigma*. These plants are genotypically $\mathbf{W_1w_3g_4}$. They have self-coloured flowers mostly of a peculiar dull shade never met with in diploids (see Plate XX, fig. 7). Sometimes, however, they are difficult or impossible to separate from full colours except by breeding. As in class (3) the flowers may have a magenta and red shade respectively.

In addition to these classes there will, of course, appear some full-coloured magenta or red flowered plants ($\mathbf{w_4}$).

The difficulty of demonstrating the segregation of this gene in tetraploid plants is obvious. The records given in the following tables are all from one particular year, 1925, when special care had been taken the year before of making up the F_1 plants in an adequate way. Even so an approximately correct classification would have been an impossibility had it not been for the experience obtained during the preceding years.

The experiments were arranged in two series, one in which red stigma was excluded, both parents being pure for green stigma, and another in which one parent had red stigma while the other had a pure green stigma. The white varieties used all proved to have pure magenta as their ground colour.

In the first case plants used for selfing and back-crossing came from the cross white, green stigma ($\mathbf{W_4B_4G_4}$) × red, green stigma ($\mathbf{w_4b_4G_4}$), all the F_1 plants being $\mathbf{W_2w_2B_2b_2G_4}$. In F_2 and back-crosses from these plants the following segregation ratios would be expected:

	White + tinged white	Magenta lavender	Red lavender	Magenta	Red	n
Back-cross:	6	20	4	5	1	36
F_2	972	280	8	35	1	1296

Tables XV and XVI show that the actual numbers are in good agreement with expectation, especially those for the back-cross.

Adding up the classes containing **W** and the classes which contain only full-coloured plants ($\mathbf{w}_4$)[1] we get (from Table XV) 81 whites : 18 coloured, which can evidently be taken to represent a 5 : 1 ratio; expectation being 82·5 whites : 16·5 coloured plants. In the same way Table XVI gives 441 whites : 8 coloured, while 436·5 whites : 12·5 coloured would be expected from a 35 : 1 ratio. The numbers prove beyond doubt that random assortment takes place between the chromosomes carrying **W**.

The next series of experiments included also **g** for red stigma, whereby several new colour-shades were introduced. Crosses were made between

TABLE XV.

Dominant white.

$\mathbf{W_2w_2B_2b_2G_4 \times w_4b_4G_4}$.

Family	No. of plants tested	White + tinged white	Lavender: Magenta	Lavender: Red	Magenta	Red
141–25	2	11	25	6	9	3
234–25	2	7	32	—	5	1
Total	4	18	57	6	14	4
Expected		16·5	55·0	11·0	13·7	2·8

TABLE XVI.

Dominant white.

$\mathbf{W_2w_2B_2b_2G_4}$ selfed.

Family	No. of plants tested	White + tinged white	Lavender: Magenta	Lavender: Red	Magenta	Red
141–25	6	189	56	2	3	1
142–25	1	34	6	—	—	—
234–25	2	128	26	—	4	—
Total	9	351	88	2	7	1
Expected		336·9	97·0	2·7	12·1	0·3

pure whites ($\mathbf{W_4B_4G_4}$) and red, red stigma ($\mathbf{w_4b_4g_4}$), all the F_1 plants being white (or tinged white) with green stigma of the constitution $\mathbf{W_2w_2B_2b_2G_2g_2}$. The purpose of these experiments was to verify the genotype of the different shades outlined above. It was, however, soon realised that far bigger numbers are wanted to get the eight or ten distinguishable classes in approximately correct proportions. The result is, moreover, rendered still more complicated by the linkage existing between **B** and **G**. The experiment therefore will have to be repeated on a much larger scale.

The only result from these last experiments then was the observation

[1] The lavenders are to be reckoned as "white" (**W**) plants.

that most of the expected classes appeared, although some of them were represented by very small numbers. An accurate analysis would of course include the testing of their genotypes by breeding, a procedure which lack of time prevented me from carrying out.

Tables XVII and XVIII give the F_2 and back-cross numbers as they were found to be distributed between the three collective classes, white, lavender and full colour. The object was to check the result already obtained from the first series of experiments.

TABLE XVII.

Dominant white.

$\mathbf{W_2w_2B_2b_2G_2g_2}$ selfed.

Family	No. of plants tested	White + tinged white	Lavender	Full colour
144–25	4	183	62	8
145–25	1	38	10	3
155–25	3	142	42	4
Total	8	363	114	15
Expected on a 27 : 8 : 1 basis		369·0	109·3	13·7
$M=$		10·0	9·2	3·7
Dev./$M=$		0·6	0·5	0·3

TABLE XVIII.

Dominant white. Back-crosses.

$\mathbf{W_2w_2B_2b_2G_2g_2 \times w_4b_4g_4}$.

Family	No. of plants tested	Tinged whites	Lavender	Full colour
144–25	3	17	33	13
145–25	1	4	12	1
155–25	2	22	76	24
Total	6	43	121	38
Expected on a 1 : 4 : 1 basis		33·7	134·6	33·7
$M=$		5·3	6·8	5·3
Dev./$M=$		1·7	2·0	0·8

The numbers obtained by selfing are seen to be in very good agreement with expectation. Back-cross numbers are, however, less satisfactory, probably due to the greater difficulty of classification met with in these crosses. In F_2 the easier distinguishable classes are in the majority and, therefore, the results from adding up the different classes into the three here specified are more reliable. In back-crosses the intermediate overlapping forms are far more abundant, making the grouping of the plants in these classes more difficult.

Both in F_2 and in back-crosses the ratio of whites to coloured comes

very near to expectation. F_2 gave, as seen from Table XVII, 477 whites: 15 coloured, while from a 35 : 1 ratio, 478·3 whites : 13·7 coloured would be expected. Back-crosses gave 164 whites : 38 coloured against the expected 5 : 1 ratio of 168·3 whites : 33·7 coloured. Both crosses accordingly strongly support the conclusions already arrived at, that chromosomes carrying **W** are distributed at random.

Sinensis *and* stellata. (**Ch**–**ch**.)

One more flower character will be mentioned only to show the great range of variation sometimes met with in tetraploids, even if but one gene and its allelomorph are involved. Correct classification is here impossible, and one could easily get the impression of more factors being at work had it not been for the knowledge that only one is responsible for the result.

There are two kinds of flower-shape known in the diploid *P. sinensis*, the ordinary *sinensis* and the star or *stellata* shape. In the former the petals have cut edges (see Plate XX, figs. 1 and 3–7) and a calyx of cylindrical shape with numerous teeth (see Plate XXI, fig. 2). *Stellata* flowers, on the contrary, have heart-shaped petals with a simple median notch (Plate XX, fig. 2), while the calyx is narrower towards the top and has only five teeth, corresponding to the number of petals (see Plate XXI, fig. 3). Further, the two forms are characterised by differences in their habit of inflorescence, the *sinensis* plants having a markedly condensed inflorescence compared to the tiering habit of the *stellata* plants.

The difference between the two varieties is, as shown by Gregory (1911), monofactorial. The hybrids are slightly intermediate in flower-shape and more pronouncedly intermediate in habit of inflorescence. There is, however, in diploids no difficulty in separating pure recessives from dominant and intermediate classes.

In tetraploids, on the contrary, classification is extremely difficult. F_2 from the cross, pure dominant × pure recessive, will exhibit a continuous sequence of transitional forms ranging from pure *sinensis* through all kinds of intermediates as regards petals, calyx and habit, to pure *stellatas*. This is chiefly due to the great variability of the heterozygotes of the type $\mathbf{Ch}_1\mathbf{ch}_3$. Plants of this genotype may in phenotype even overlap the pure recessives, making classifying altogether uncertain.

During the first years of my working with *P. sinensis* I tried very hard to separate the different classes, carefully examining both petals and calyx of each plant. Eventually I gave up this character as being not good enough for using in experiments. The only way of classifying would

be to test a great many plants by breeding, a procedure which, however, would require too much time and space.

Table XIX gives the result of some efforts in classifying F_2 plants, where an attempt has been made to sort out the pure recessives on their phenotype alone.

The excess of pure recessives is probably due to the overlapping of $\mathbf{Ch_1ch_3}$ forms. It is not safe from a result like this to draw any conclusions as regards the behaviour of the chromosomes carrying this gene.

TABLE XIX.

Sinensis–stellata.

Family	No. of plants tested	*Sinensis* + intermediate	*Stellata*
121–24	4	83	6
150–25	3	254	8
141–25	5	228	13
142–25	2	41	2
Total	14	606	29
Expected on a 35 : 1 ratio		617·4	17·6

"*Primrose Queen*" *eye*. (Q–q.)

The only time I had the opportunity of observing the appearance of a tetraploid mutant was in the case of a variety "Primrose Queen" eye. This plant came in a diploid family (21–22) pure for dominant white, and for the recessive character called "Primrose Queen" eye. In an otherwise very uniform family the plant at once struck one as being of much coarser build. Chromosome counts from root tips gave 48 chromosomes, proving the plant to be as expected of tetraploid constitution.

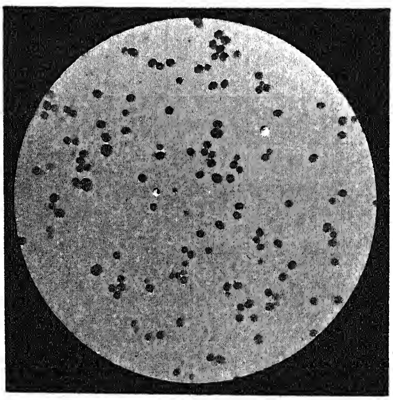
The most striking feature of this new tetraploid was its marked sterility. In 1922, the year of its origin, the plant failed altogether as a female, regardless of whether it was fertilised by own pollen or by pollen from other tetraploids. Used as a male in crosses with other tetraploid plants 12 seeds were obtained; only one of these started germinating, but the seedling had not enough vitality to throw off its seed coat, and soon perished. With diploid plants crosses failed, as expected, altogether. The pollen of the new mutant is, as seen in Text-fig. 1, rather irregular, but in its main features not unlike the pollen of long-styled plants. Its germination power was not tested.

The plant was carefully nursed and, in the spring of 1923, was large enough to be divided into three plants, all of which were tried both as males and females. This time nine seeds were obtained from selfing, none

of which, however, germinated. Using it as a male, however, I now succeeded in getting three F_1 plants.

The original mutant was kept for a third year and a few more F_1 plants were obtained, always by using the new plant as a male. As a female the plant never gave any seed capable of developing. Whether this sterility is a general feature of new tetraploids is, so far, unknown. But there is no obvious reason why this case should form an exception. Possibly the chromosomes require some time to get used to their new fourfold condition.

The F_1 plants proved to be comparatively fertile, although they never gave large families. Extracted homozygous "Primrose Queen" eye plants also were moderately fertile.



Text-fig. 3. Pollen from a "Primrose Queen" eye plant.

The gene for "Primrose Queen" eye is of special interest, in so far as it affects different parts of the flower in a peculiar way. The "eye" of the *Primula* flower generally occupies a small area round the mouth of the corolla tube. The variety "Primrose Queen" has, as seen in Plate XXI, fig. 1, a much larger eye, the yellow colour extending over about a third to a half of the petal. More remarkable is the change in form and position of the stigma caused by this gene; the flowers are "homostyled"; as in long-styled flowers the anthers are found at the bottom of the corolla tube; the stigma, however, which in the case of long-styledness should appear at the opening of the tube, is short and does not protrude between the anthers; the stigma, too, is drawn out into a long point (see Plate XXI, fig. 2). Gregory (1911) found that, in diploids, homostyle plants of this kind are genetically long-styled. The peculiar form and position of the

stigma was, in diploids, found never to be separated from the large yellow eye; the gene for "Primrose Queen" eye, therefore, presumably affects the pistil of long-styled plants. Short-styled plants with the large yellow eye are perfectly normal both as regards anthers and stigma.

Tetraploid plants, homozygous for **q**, exhibit the same peculiarities; the style was found to be slightly longer in flowers of the *stellata* type (compare Plate XXI, figs. 2, 3), the stigma, however, in no case protruding through the anthers.

In crossings this new tetraploid gave interesting forms unknown among diploids. F_1 plants from the cross "Primrose Queen" eye × normal eye, long-style, had, as expected, normal-eyed, long-styled flowers corresponding to what we get in diploids; sometimes the stigma of F_1 flowers may be larger and flatter and slightly pointed, this being most conspicuous among the first flowers opening (see Plate XXI, fig. 8). In F_2 and back-crosses a new type appeared, namely, *homostyled plants with normal eye*. These plants were at once suspected to be heterozygotes of the type $\mathbf{Q_1q_3}$, a theory which proved to be right (see Tables XXII and XXIII below). The fact, therefore, was revealed that whereas three doses of **q** are sufficient to produce the peculiar type of pistil, four doses of **q** are necessary to give the large yellow eye as well. A homostyle normal-eyed flower is pictured in Plate XXI, figs. 4, 5, 7: fig. 4 shows the normal-shaped eye, fig. 5 the position of the anthers, and fig. 7 the shape of the pistil; the style is somewhat longer than in $\mathbf{q_4}$ flowers, but does not show above the corolla tube (compare the length of the style in figs. 6 and 8 giving the normal long-styled type and the $\mathbf{Q_2q_2}$ type respectively). These heterozygotes ($\mathbf{Q_1q_3}$) are, however, subject to a great deal of variation, the later flowers on the same plant very often having apparently normal long-styled flowers. Probably, therefore, $\mathbf{Q_1q_3}$ plants exist, having nothing but normal flowers.

Table XX gives the result of selfing plants of the type $\mathbf{Q_2q_2}$. All plants in this, as well as Table XXI, are F_1 plants.

Owing to the above-described characteristics of the $\mathbf{Q_1q_3}$ heterozygotes it is here possible to distinguish three classes. The pure recessive class ($\mathbf{q_4}$) comes, as seen, according to expectation. The middle class is too small, a result which is probably due to the above-mentioned variability of this type. Correspondingly the first class is somewhat too big.

This discrepancy between expected and actual numbers is still more pronounced in Table XXI, which gives back-crosses from the same plants.

The first class of Table XXI is, as seen, far too big, while the second

class, containing plants of the homostylic phenotype, is too small. The pure recessive class, on the other hand, agrees very well with expected numbers.

Adding up classes containing one or more dominants and comparing them to the numbers of pure recessives we get from selfing (Table XX) 189Q : 8q, while the expected numbers in case of random assortment of the chromosomes would be 191·5 Q : 5·5q, a fairly good agreement. Back-crosses (Table XXI) are still more strikingly in accordance with expectation, giving 88Q : 17q, compared to 87·5Q : 17·5q, the number expected from a 5 : 1 ratio. One may safely conclude that the chromosomes carrying Q are distributed at random, regardless of the way in which they entered the plant.

TABLE XX.

"*Primrose Queen*" *eye.*

Q_2q_2 selfed.

Family	No. of plants tested	Normal eye, long-style ($Q_4+Q_3+Q_2$)	Normal eye, homostyle (Q_1q_3)	"Primrose Queen" eye, homostyle (q_4)
111–24	2	6	1	1
146–25	1	8	2	—
183–25	1	2	1	—
187–25	1	2	1	—
148–26	2	13	2	—
149–26	2	18	12	3
306–26	1	45	3	—
154–26	4	64	9	4
Total	14	158	31	8
Expected on a 27 : 8 : 1 basis		148·5	43·0	5·5
$M=$		6·0	5·8	2·3
Dev./$M=$		1·6	2·1	1·0

TABLE XXI.

"*Primrose Queen*" *eye.*

Q_2q_2 back-crossed.

Family	No. of plants tested	Normal eye, long-style (Q_2q_2)	Normal eye, homostyle (Q_1q_3)	"Primrose Queen" eye, homostyle (q_4)
111–24	2	5	3	1
146–25	2	14	14	9
183–25	1	3	3	—
187–25	1	2	2	1
148–26	2	3	1	1
149–26	2	16	11	4
154–26	3	7	4	1
Total	13	50	38	17
Expected on a 1 : 4 : 1 basis		17·5	70	17·5
$M=$		3·8	4·3	3·8
Dev./$M=$		8·5	7·4	0·1

So far five plants, homostyled with normal eye, have been tested. There can be no doubt about these plants being constitutionally Q_1q_3.

The actual numbers come very near to the expected 3 : 1 and 1 : 1 ratios. The eight plants of Table XXIII with long-style are no doubt only plus-variants, although not tested, showing that Q_1q_3 plants overlap towards the normal condition.

TABLE XXII.

"Primrose Queen" eye.

Q_1q_3 selfed.

Family	No. of plants tested	Normal eye, long-style (Q_2q_2)	Normal eye, homostyle (Q_1q_3)	"Primrose Queen" eye, homostyle (q_4)
185–25	1	16	10	5
184–26	1	1	3	—
186–26	2	—	6	2
187–26	1	18	12	6
Total	5	35	31	13
Expected on a 1 : 2 : 1 basis		19·8	39·5	19·8
$M=$		3·9	4·4	3·9
Dev./$M=$		3·9	1·5	3·9

TABLE XXIII.

"Primrose Queen" eye.

Q_1q_3 back-crossed.

Family	No. of plants tested	Normal eye, long-style	Normal eye, homostyle (Q_1q_3)	"Primrose Queen" eye, homostyle (q_4)
185–25	1	7	15	20
184–26	1	1	9	3
186–26	2	—	8	4
187–26	1	—	8	17
Total	5	8	40	44
Expected on a 1 : 1 basis		0	46	46
$M=$		—	4·8	4·8
Dev./$M=$		—	1·3	0·4

Fern leaf. (P–p.)

A great many different leaf shapes are known among diploid *P. sinensis*. So far but two of these, "fern" and "moss-curl," have mutated to the tetraploid condition. The present paper only deals with the first-mentioned of these characters.

In the diploid form fern leaf is, as shown by Gregory (1911) and confirmed by all later experiments, a pure recessive, determined by one pair of genes. The cross, fern × palm (the normal leaf shape), gives normal-

leaved plants only, which, when selfed, segregate in a straight 3 : 1 ratio.

In tetraploids, on the other hand, a curious intermediate type appears in F_2's and back-crosses, due to the incapability of one **P** to show complete dominance in the presence of three recessive allelomorphs. Gregory (1914) mentions these intermediates between the palmate and fern leaf, and his notes show that he, no doubt, suspected their genotype. The phenomenon is the same as earlier described, especially in the case of "Primrose Queen" eye, only here the intermediate class appears to be more distinct.

The cross, pure fern × pure palm, shows, as in diploids, complete dominance of the palmate leaf shape. In F_2 and back-crosses one gets, however, as just mentioned, in addition to the parental types, plants having leaves of a curious kind of intermediate shape. These leaves are characterised by having extra lobes or leaflets down the stem, completely separated from the main part of the leaf. A great deal of variation exists regarding the shape of the main leaf and the number of leaflets. Plate XXII, figs. 1 and 3 show the elongated shape of the pure fern leaf compared with the broad shape of the normal palmate leaf. Underneath are pictured three examples of the intermediate type. Plate XXII, fig. 4 at once suggests the fern leaf, but differs from this by being much more cut up, showing two pairs of free leaflets. In Plate XXII, fig. 5 the main part of the leaf is more towards the palmate shape; a conspicuous extra lobe or leaflet is seen to the right. The third leaf (Plate XXII, fig. 6) has a complete palmate shape, only a tiny extra leaflet to the right betrays its genotype. The class may, in a few cases, overlap the normal class, while overlapping has never been found in the direction of fern leaf. Different leaf shapes may appear on the same plant as exhibited by Plate XXIII. Two leaves bending down are seen to have a very nearly palmate shape except for the one conspicuous extra leaflet being present in both. A younger leaf standing upright to the left is the same as pictured in Plate XXII, fig. 4. Breeding tests showed that these plants were of the expected $\mathbf{P}_1\mathbf{p}_3$ constitution.

Table XXIV gives the results of selfing $\mathbf{P}_2\mathbf{p}_2$ plants. The first four families of the table all consist of F_1 plants produced by crossing pure palm ($\mathbf{P}_4$) and pure fern ($\mathbf{p}_4$); their genotype accordingly must be $\mathbf{P}_2\mathbf{p}_2$, barring any chromosomal aberrations. The last two plants of the table were taken from an F_2; they both had palmate leaves with no extra lobes, and were found by back-crossing to be of the $\mathbf{P}_2\mathbf{p}_2$ constitution (see Table XXV).

When scoring, three classes were recognised, plants with palmate leaves, plants with leaves of the intermediate type, characterised by having extra lobes, and plants with leaves of the fern type. The distribution of the three classes should be in the ratio 27 : 8 : 1. The actual numbers are, as seen, in good agreement with their expectation; the fern class comes exactly right while the palm class is slightly too large and the extra lobe class slightly too small; this no doubt is due to the overlapping of the last-mentioned class towards the palm class. Comparing fern plants to not-fern plants we should expect a 35 : 1 ratio. We get

TABLE XXIV.

Palm leaf–fern leaf.

P_2p_2 selfed.

Family	No. of plants tested	Palm	Extra lobes	Fern
182–21	1	6	1	1
141–25	1	26	—	1
142–25	1	28	9	3
156–25	4	148	36	4
130–25	2	85	28	1
Total	9	293	74	10
Expected on a 27 : 8 : 1 basis		282·7	83·8	10·5
	$M=$	8·4	7·9	3·2
	Dev./$M=$	1·2	1·2	0·1

TABLE XXV.

Palm leaf–fern leaf.

P_2p_2 back-crossed.

Family	No. of plants tested	Palm	Extra lobes	Fern
182–21	1	10	8	5
156–25	3	7	15	4
130–25	2	10	26	9
Total	6	27	49	18
Expected on a 1 : 4 : 1 basis		15·7	62·6	15·7
	$M=$	3·6	3·8	3·6
	Dev./$M=$	3·1	3·6	0·6

367 palms + extra lobes to 10 ferns or a ratio of 35·05 : 0·95. Chromosomes carrying **P** are accordingly distributed at random.

The result from back-crossing these P_2p_2 plants is given in Table XXV. Numbers are rather small but agree with the conclusion arrived at above. Again the palm class is too big, while the fern class comes very near to expectation. Adding up we get 76 palms + extra lobes to 18 ferns, giving a ratio of 4·2 : 1, instead of the expected 5 : 1 ratio; numbers are, however, too small for expecting a closer agreement.

A series of plants showing the intermediate types was tested partly by selfing, partly by back-crossing to fern. Every plant tested proved to be of the $\mathbf{P}_1\mathbf{p}_3$ constitution. The results of these experiments are set out in Tables XXVI and XXVII.

Numbers came fairly close to expectation and exhibit the same peculiarity as met with above, namely the appearance of too many palm

TABLE XXVI.

Palm leaf–fern leaf.

$\mathbf{P}_1\mathbf{p}_3$ selfed.

Family	No. of plants tested	Palm	Extra lobes	Fern
112–23	2	4	8	1
113–23	1	2	2	2
114–23	2	3	2	2
115–23	1	11	23	1
118–23	1	1	3	3
153–24	1	9	10	4
130–25	3	32	38	31
145–25	1	12	26	14
154–26	3	18	37	18
Total	15	92	149	76
Expected on a 1 : 2 : 1 basis		79·3	158·5	79·3
$M=$		7·7	8·9	7·7
Dev./$M=$		1·6	1·1	0·4

TABLE XXVII.

Palm leaf–fern leaf.

$\mathbf{P}_1\mathbf{p}_3$ back-crossed.

Family	No. of plants tested	Palm	Extra lobes	Fern
112–23	2	1	8	2
113–23	1	2	1	3
114–23	1	—	5	2
115–23	1	3	28	26
153–24	1	—	18	12
130–25	3	—	32	45
145–25	1	—	9	10
Total	10	6	101	100
Expected on a 1 : 1 basis		—	103·1	103·1
$M=$		—	7·2	7·2
Dev./$M=$		—	0·3	0·5

plants. Back-crosses are here of particular interest, for they gave in addition to the expected classes six plants having palm leaves. One may safely conclude that these plants are of the $\mathbf{P}_1\mathbf{p}_3$ genotype, as other genotypes are excluded by the type of the cross. The only other way of explaining these six plants would be by assuming non-disjunction or some other kind of chromosomal disturbance. It is, however, more natural

and more in agreement with the above to regard them as overlapping $\mathbf{P_1p_3}$ plants. Unfortunately their genetical constitutions were not tested by breeding.

Summing up, the experiments given above show that at least six different genes are distributed at random. The seventh gene investigated, that for *sinensis* flower (**Ch**), wants further examination, owing to the overlapping tendencies of its heterozygotes. Three of the genes ($\mathbf{S_1}$, **B** and **G**) are linked and, therefore, belong to the same group of chromosomes. The experiments accordingly show that the chromosomes of at least four of the twelve groups, each containing four homologous chromosomes, are distributed at random, thus proving that homologous chromosomes coming from the same parent conjugate as easily as those coming from opposite parents.

Linkage in tetraploids.

In the ordinary diploid variety of *P. sinensis* two linkage groups have so far been recognised. One of these containing in diploids at least four genes, is at present known also in the tetraploid form, the group here, however, so far containing only three genes. The monofactorial distribution of these genes has been described above; in the following their inter-relationship, as brought out by the experiments, will be given. To my knowledge this is the first time linkage has been described in a tetraploid form. The genes involved are those for *short-style* (**S**) versus *long-style* (**s**), *magenta flower colour* (**B**) versus *red colour* (**b**), and *green stigma* (**G**) versus *red stigma* (**g**). It has already been shown that in tetraploids, as in diploids, **S** and **G** show complete dominance, whereas **B** in tetraploids, when present only in a single dose ($\mathbf{B_1b_3}$), shows incomplete dominance, giving flowers of a reddish shade. It has further been demonstrated that all three genes, when present in double doses ($\mathbf{A_2a_2}$), give a clear 35 : 1 ratio from selfing and a 5 : 1 ratio from back-crosses, thus proving a random assortment of the four homologous chromosomes carrying these genes.

Several questions at once present themselves in connection with the problem of linkage. Firstly, is the crossing-over percentage unchanged in the tetraploid variety, or is the linkage in tetraploids of a different strength from that found in diploids? Secondly, the question arises whether crossing-over will take place equally well between any two of the four homologous chromosomes. From the monofactorial distribution of the genes we know that the four chromosomes in question pair at random,

that is, pairing takes place equally well between chromosomes from opposite as between those from same parent; but it does not follow that crossing-over takes place according to the same rule. These are some of the questions which the following experiments try to answer.

Linkage in tetraploids of the kind here described will be of a far more complicated nature than in the diploids from which they arose. Even when considering two pairs of the genes only, a great many possibilities exist as regards their distribution among the four homologous chromosomes. Calling the dominant genes **A** and **B**, their recessive allelomorphs **a** and **b** respectively, the following scheme shows the manifold ways in which these genes, when present in one or two doses, may enter a plant. In every case the chromosomes coming from one parent are written above the line, those coming from the other parent below the line:

Case I. Four dominant genes:

$$\left.\begin{array}{ll}(1) & \frac{\mathbf{AB}}{\mathbf{ab}}\,\frac{\mathbf{AB}}{\mathbf{ab}},\quad \frac{\mathbf{AB}}{\mathbf{AB}}\,\frac{\mathbf{ab}}{\mathbf{ab}}\\[1ex] (2) & \frac{\mathbf{AB}}{\mathbf{aB}}\,\frac{\mathbf{Ab}}{\mathbf{ab}},\quad \frac{\mathbf{AB}}{\mathbf{Ab}}\,\frac{\mathbf{ab}}{\mathbf{aB}},\quad \frac{\mathbf{AB}}{\mathbf{Ab}}\,\frac{\mathbf{aB}}{\mathbf{ab}}\\[1ex] (3) & \frac{\mathbf{Ab}}{\mathbf{aB}}\,\frac{\mathbf{Ab}}{\mathbf{aB}},\quad \frac{\mathbf{Ab}}{\mathbf{Ab}}\,\frac{\mathbf{aB}}{\mathbf{aB}}\end{array}\right\}\begin{array}{l}\mathbf{A}_2\mathbf{a}_2\\ \mathbf{B}_2\mathbf{b}_2\end{array}.$$

Case II. Three dominant genes:

$$\left.\begin{array}{ll}(1) & \frac{\mathbf{AB}}{\mathbf{ab}}\,\frac{\mathbf{Ab}}{\mathbf{ab}},\quad \frac{\mathbf{AB}}{\mathbf{Ab}}\,\frac{\mathbf{ab}}{\mathbf{ab}}\\[1ex] (2) & \frac{\mathbf{Ab}}{\mathbf{aB}}\,\frac{\mathbf{Ab}}{\mathbf{ab}},\quad \frac{\mathbf{Ab}}{\mathbf{Ab}}\,\frac{\mathbf{aB}}{\mathbf{ab}}\end{array}\right\}\begin{array}{l}\mathbf{A}_2\mathbf{a}_2\\ \mathbf{B}_1\mathbf{b}_3\end{array}.$$

$$\left.\begin{array}{ll}(3) & \frac{\mathbf{AB}}{\mathbf{ab}}\,\frac{\mathbf{aB}}{\mathbf{ab}},\quad \frac{\mathbf{AB}}{\mathbf{aB}}\,\frac{\mathbf{ab}}{\mathbf{ab}}\\[1ex] (4) & \frac{\mathbf{Ab}}{\mathbf{aB}}\,\frac{\mathbf{aB}}{\mathbf{ab}},\quad \frac{\mathbf{Ab}}{\mathbf{ab}}\,\frac{\mathbf{aB}}{\mathbf{aB}}\end{array}\right\}\begin{array}{l}\mathbf{A}_1\mathbf{a}_3\\ \mathbf{B}_2\mathbf{b}_2\end{array}.$$

Case III. Two dominant genes:

$$\left.\begin{array}{ll}(1) & \frac{\mathbf{AB}}{\mathbf{ab}}\,\frac{\mathbf{ab}}{\mathbf{ab}}\\[1ex] (2) & \frac{\mathbf{Ab}}{\mathbf{aB}}\,\frac{\mathbf{ab}}{\mathbf{ab}},\quad \frac{\mathbf{Ab}}{\mathbf{ab}}\,\frac{\mathbf{aB}}{\mathbf{ab}}\end{array}\right\}\begin{array}{l}\mathbf{A}_1\mathbf{a}_3\\ \mathbf{B}_1\mathbf{b}_3\end{array}.$$

In each case the formation of gametes takes place in one characteristic ratio for each configuration. I have not thought it necessary to give

the gametes possible in each separate case, but have only considered those arrangements which are present in the experiments.

When studying linkage in tetraploids, it is obviously of the greatest importance to know accurately in what way the genes involved entered the plant. Even with known parentage, however, the constitution of a plant is not always easily predicted. Any configuration, for instance, in which the chromosomes **Ab** and **aB** came from one parent, cannot be predicted with certainty because of the possibility of crossing-over in the parent plant. In the following experiments no plant has been used unless the genotype of its parents was well known and, as far as possible, only plants made up by certain crossings have been considered, viz. crossings which made it possible to know for certain the arrangement of the genes in the daughter plants.

In discussing the results given in the tables below I have preferred to measure the strength of the linkage in terms of the gametic ratio, instead of using the percentage of cross-over plants. The reason for this is that most of the classes appearing in F_2's and back-crosses will contain both cross-over and non-cross-over plants; as will soon be evident it is in cases like this easier to calculate the expected number by means of the gametic ratio. In diploids the linkage existing between the three pairs of genes here studied, according to Gregory, de Winton and Bateson (1923), are:

S–B,	♀ 12·2 : 1 or 7·5 per cent.,	♂ 7 : 1 or 12·5 per cent.
S–B,	♀ 12·2 : 1 or 7·5 ,,	♂ 7 : 1 or 12·5 ,,
S–G,	♀ 2 : 1 or 33·3 ,,	♂ 1·5 : 1 or 40 ,,
B–G,	♀ 2·2 : 1 or 31·3 ,,	♂ 1·9 : 1 or 34·5 ,,

the order of the genes being **S–B–G.**

In the following the chromosomes coming from the mother are always written above the line, those coming from the father below the line, or conversely.

Case I.

$$(3)\ \frac{\mathbf{Ab}}{\mathbf{aB}}\frac{\mathbf{Ab}}{\mathbf{aB}}.\ \text{Four dominants.}$$

The gametes formed by plants of this constitution are found by considering every possible arrangement of the four chromosomes in question during the maturation of the germ cells. Giving the genes involved the indexes 1 and 2, one sees that theoretically the chromosomes may pair in three different ways:

$$(1)\ \frac{\mathbf{A_1b_1}}{\mathbf{a_1B_1}}\frac{\mathbf{A_2b_2}}{\mathbf{a_2B_2}};\quad (2)\ \frac{\mathbf{A_1b_1}}{\mathbf{a_2B_2}}\frac{\mathbf{A_2b_2}}{\mathbf{a_1B_1}};\quad (3)\ \frac{\mathbf{A_1b_1}}{\mathbf{A_2b_2}}\frac{\mathbf{a_1B_1}}{\mathbf{a_2B_2}}.$$

In the first two of these arrangements, which are virtually alike, pairing takes place between chromosomes from opposite parents, whereas the third of these arrangements represents pairing between chromosomes from the same parent. In (1) and (2) the gametes may be found by using the ordinary chess-board method, the gamete formation here paralleling the formation of zygotes from a selfed diploid plant of the constitution $\frac{\mathbf{Ab}}{\mathbf{aB}}$. If the linkage is represented by the ratio $x:1$ we get the gametes:

	AB	x**Ab**	x**aB**	**ab**
AB	**AB**	x**AB**	x**AB**	**AB**
x**Ab**	x**AB**	x^2**Ab**	x^2**AB**	x**Ab**
x**aB**	x**AB**	x^2**AB**	x^2**aB**	x**aB**
ab	**AB**	x**Ab**	x**aB**	**ab**

i.e. $(2x^2 + 4x + 3)\,\mathbf{AB} + (x^2 + 2x)\,\mathbf{Ab} + (x^2 + 2x)\,\mathbf{aB} + \mathbf{ab}$,[1]

the total amount of gametes being $4x^2 + 8x + 4$.

Case I (3), or pairing between chromosomes from the same parent, gives nothing but **AB** gametes, crossing-over if such takes place making no difference to the final result. Since the chance for this kind of pairing is only half as big as the chance of pairing between chromosomes from opposite parents, we shall have to add $(2x^2 + 4x + 2)$ **AB** gametes, the total amount of gametes being represented by

$$(4x^2 + 8x + 5)\,\mathbf{AB} + (x^2 + 2x)\,\mathbf{Ab} + (x^2 + 2x)\,\mathbf{aB} + \mathbf{ab}.$$

The **ab** class here represents the only pure cross-over class. In any of the first three classes of gametes the dominant genes may be present in single or double dose.

From the preceding it follows that breeding from plants of this constitution will throw light upon questions concerning crossing-over between chromosomes coming from opposite parents. It is, on the other hand, an advantage that cross-overs between chromosomes coming from the same parent are in this case not recognisable; these phenomena may, as seen, be studied from other genotypes.

F_1 plants of this type have been made only once by crossing plants homozygous for red flower colour and green stigma ($\mathbf{b}_4\mathbf{G}_4$) with plants of the genotype $\mathbf{B}_3\mathbf{b}_1\mathbf{g}_4$. The F_1 plants were accordingly of two kinds, $\frac{\mathbf{bG}\ \mathbf{bG}}{\mathbf{Bg}\ \mathbf{Bg}}$ and $\frac{\mathbf{bG}\ \mathbf{bG}}{\mathbf{Bg}\ \mathbf{bg}}$. In this connection the former only of these types is of interest, the latter will be dealt with later on. Numbers from back-

[1] For brevity the complete formula of each gamete is not given, but only its "phenotypical expression."

crossing three plants all used as females are given in Table XXVIII. There is a shortness of red-flowered plants, the proportion of magentas to reds being 8·2 : 1 instead of 5 : 1. In calculating the expected numbers, therefore, magentas and reds have been treated separately.

The linkage **B**–**G** in diploids is, as mentioned above, on the female side given by the gametic ratio 2·2 : 1. Introducing this value into the formula given above, we should expect the distribution of the classes to be 41·9**BG** + 9·2**Bg** + 9·2**bG** + **bg**. The expected numbers calculated on this basis are, as seen, in perfect agreement to the numbers actually obtained. As regards chromosomes originating from opposite parents, the strength of the linkage between magenta flower colour and green stigma is apparently unchanged, crossing-over taking place at the same rate as in diploids.

Even with an agreement as strikingly pronounced as the one shown in Table XXVIII one has, however, to be careful about arriving at too

TABLE XXVIII.

Case I (3). *Female back-crosses.*

$$\frac{\mathbf{Bg}}{\mathbf{bG}}\frac{\mathbf{Bg}}{\mathbf{bG}} \times \mathbf{b}_4\mathbf{g}_4.$$

Family	No. of plants tested	**BG**	**Bg**	**bG**	**bg**
114–24	3	106	22	14	2
Expected on a 2·2 : 1 basis		104·9	23·1	14·4	1·6
$M =$		9·4	4·4	3·6	1·3
Dev./$M =$		0·1	0·2	0·1	0·3

definite conclusions. By applying different linkage values one will soon see that even big departures from the value found in diploids will not noticeably change the size of the first classes. As regards the double recessive class, the only pure cross-over class, the actual numbers obtained in this experiment are too small for definite conclusions. A few examples will perhaps elucidate this. Let us first consider a possible strengthening of linkage. If, for instance, the linkage has changed from 2·2 : 1 to 5 : 1 (or from 31 to 17 per cent.) the distribution of the classes would be 145**BG** + 35**Bg** + 35**bG** + **bg** or, for the present case,

$$103{\cdot}1\,\mathbf{BG} + 24{\cdot}9\,\mathbf{Bg} + 15{\cdot}6\,\mathbf{bG} + 0{\cdot}4\,\mathbf{bg},$$

numbers which do not disagree with the ones actually obtained. A change of the linkage in the other direction, a weakening of the linkage, would be equally difficult to trace, even a cross-over percentage of 50 still being within the limits of probability. The expected numbers would, in this case, be 108·8**Bg** + 19·2**Bg** + 12**bG** + 4**bg**. The object of this

discussion is to emphasise how cautious one has to be, and the difficulties one meets when dealing with material like the present. The numbers given in Table XXVIII are far too small for a definite settlement of the question. One can only say that the actual numbers agree closely with the expected ones, calculated on the basis that crossing-over takes place at the same rate as in diploids between chromosomes coming from opposite parents. From this, however, one cannot infer that the linkage value is identical.

Case II.

$$(1)\ \frac{\mathbf{AB}}{\mathbf{ab}}\frac{\mathbf{Ab}}{\mathbf{ab}}.\ \text{Three dominants.}$$

The gametes theoretically formed by plants of this genotype may be found by means of the chess-board method, as described in the foregoing case, or simply by the following reasoning:

Pairing between chromosomes from opposite parents will result in the formation of the following gametes:

$$\text{Non-cross-overs: } 2\mathbf{AB} + \mathbf{Ab} + \mathbf{ab},$$
$$\text{Cross-overs: } \mathbf{AB} + 2\mathbf{Ab} + \mathbf{aB}.$$

If the linkage is represented by the gametic ratio $x : 1$ the total amount of gametes formed by this arrangement of the chromosomes will equal

$$x\,(2\mathbf{AB} + \mathbf{Ab} + \mathbf{ab}) + (\mathbf{AB} + 2\mathbf{Ab} + \mathbf{aB})$$
$$= (2x + 1)\,\mathbf{AB} + (x + 2)\,\mathbf{Ab} + \mathbf{aB} + x\mathbf{ab},$$

the total sum of gametes formed being $4x + 4$. Here the **aB** class represents the only pure cross-over class, while the double recessive class **ab** is a pure non-cross-over class.

In addition to these, gametes are also formed by pairing between chromosomes coming from the same parent. This arrangement will give nothing but **AB** and **Ab** gametes; crossing-over, if such takes place, will have no influence upon the final result. This kind of pairing takes place only half as many times as that between chromosomes from opposite parents, the total numbers which have to be added therefore being $(x + 1)\,\mathbf{AB} + (x + 1)\,\mathbf{Ab}$.

Altogether the gametes formed by plants of this genotype will be

$$(3x + 2)\,\mathbf{AB} + (2x + 3)\,\mathbf{Ab} + \mathbf{aB} + x\mathbf{ab}.$$

As in the foregoing case, plants of this constitution are excellently suited for studying linkage and cross-over phenomena between chromosomes coming from opposite parents, while no information can be obtained on crossing-over between chromosomes from the same parent.

Some of the experiments related below include selfing as well as back-crossing of these plants. A few words, therefore, must be said as to the forming of zygotes from selfed plants. As mentioned above, the diploid *Primula* showed a difference in strength of linkage between the male and female sides. Supposing that the linkage is expressed by the gametic ratio $x:1$ on the female side and $y:1$ on the male side, the zygotes formed by selfing may be calculated from the formula:

$$\begin{aligned}(27xy + 26x + 26y + 26)\,\mathbf{AB}\\ + (8xy + 9x + 9y + 9)\,\mathbf{Ab}\\ + (x + y + 1)\,\mathbf{aB}\\ + xy\,\mathbf{ab}.\end{aligned}$$

Turning to the experiments themselves three different arrangements of the genes **B**, **S** and **G** have been studied.

1. $\frac{\mathbf{bs}}{\mathbf{BS}}\frac{\mathbf{bs}}{\mathbf{Bs}}$. This combination of genes was obtained by crossing plants homozygous for red flower colour and long-style with plants homozygous for magenta and having only one dose of the gene for short-style ($\mathbf{b_4s_4} \times \mathbf{B_4S_1s_3}$). Obviously every plant from this cross showing short-style must be of the above genotype.

Back-crosses were made both ways, and the results of these are given in Tables XXIX and XXX. Calculation of the expected numbers is based upon the gametic ratios found in diploids respectively on the male and female sides.

TABLE XXIX.

Case II (1). *Female back-crosses.*

$$\frac{\mathbf{bs}}{\mathbf{BS}}\frac{\mathbf{bs}}{\mathbf{BS}} \times \mathbf{b_4s_4}.$$

Family	No. of plants tested	BS	Bs	bS	bs
114–24	3	97	51	1	18
Expected on a 12·2 : 1 basis		86·6	61·4	1·4	17·6
$M =$		6·0	6·0	1·1	1·
Dev./$M =$		1·7	1·7	0·4	0·4

TABLE XXX.

Case II (1). *Male back-crosses.*

$$\mathbf{b_4s_4} \times \frac{\mathbf{bs}}{\mathbf{BS}}\frac{\mathbf{bs}}{\mathbf{Bs}}.$$

Family	No. of plants tested	BS	Bs	bS	bs
114–24	2	28	14	1	7
Expected on a 7 : 1 basis		23·9	17·7	1·1	7·3
$M =$		3·5	3·4	1·0	2·4
Dev./$M =$		1·2	1·1	1·0	0·01

There is, as seen, a strong agreement between expected and actual numbers in both cases. As before (case I (3)), one cannot safely conclude, from this, that the linkage value is unchanged. Looking, however, upon the two last classes of the table, which according to the formula should give the actual gametic ratio, the maintenance of the diploid values seems to be strongly indicated as regards the difference between the female and male sides; the tables show a stronger linkage on the female side corresponding to what we find in diploids.

2. $\frac{\mathbf{GB}}{\mathbf{gb}}\,\frac{\mathbf{Gb}}{\mathbf{gb}}$. This genotype was made by crossing pure double recessives ($\mathbf{g}_4\mathbf{b}_4$) with plants homozygous in green stigma, and carrying one or more doses of red flower colour. The F_1 plants tested all proved to have only one dose of **B**, and must accordingly be of the above constitution. The double recessives were used in the making of the F_1 plants, partly as males, partly as females; in the tables, therefore, the formula means that the genes above the line came from one parent, those below the line from the other.

The result of back-crossing on the male and female sides is given in Tables XXXI and XXXII.

TABLE XXXI.

Case II (1). *Female back-crosses.*

$\frac{\mathbf{GB}}{\mathbf{gb}}\,\frac{\mathbf{Gb}}{\mathbf{gb}} \times \mathbf{g}_4\mathbf{b}_4.$

Family	No. of plants tested	**GB**	**Gb**	**gB**	**gb**
82–15	1	8	6	1	3
152–26	2	84	58	5	16
Total	3	92		6	19
Expected on a 2·2 : 1 basis		81·1	69·8	9·4	20·7
$M=$		6·7	6·5	3·3	4·4
Dev./$M=$		1·6	0·9	1·0	0·4

TABLE XXXII.

Case II (1). *Male back-crosses.*

$\mathbf{g}_4\mathbf{b}_4 \times \frac{\mathbf{GB}}{\mathbf{gb}}\,\frac{\mathbf{Gb}}{\mathbf{gb}}.$

Family	No. of plants tested	**GB**	**Gb**	**gB**	**gb**
56–14	1	12	20	3	9
85–15	1	10	8	—	—
152–26	2	36	28	1	6
Total	4	58	56	4	15
Expected on a 1·9 : 1 basis		58·9	52·0	7·6	14·5
$M=$		5·7	5·6	2·7	3·6
Dev./$M=$		0·2	0·7	1·2	0·1

The actual numbers obtained show a good agreement with the calculated numbers, a fact which points strongly to an unchanged linkage, although the numbers are too small for definitely settling this question; but even small changes in the gametic ratio will in this case make a perceptible difference in the class frequencies. As seen, a small difference exists in diploids between the linkage on the male and female sides; but to settle the question of whether this difference has been maintained in tetraploids a far greater number of back-crosses is required.

The conclusion that the linkage is the same in tetraploids as in diploids is strongly supported by the result obtained from selfing.

TABLE XXXIII.

Case II (1). *Selfed plants.*

$\frac{\mathbf{GB}}{\mathbf{gb}}\frac{\mathbf{Gb}}{\mathbf{gb}}$ selfed.

Family	No. of plants tested	**GB**	**Gb**	**gB**	**gb**
55–14	2	84	23	4	2
56–14	3	72	30	2	1
104–14	2	57	10	—	2
152–26	1	23	8	1	1
Total	8	236	71	7	6
Expected		232·0	75·0	7·1	5·9
	$M=$	8·0	7·6	2·6	2·4
	Dev./$M=$	0·5	0·5	0·04	0·04

The number of plants is here fairly high and, as seen, in striking agreement with expectation.

3. $\frac{\mathbf{GS}}{\mathbf{gs}}\frac{\mathbf{Gs}}{\mathbf{gs}}$. Plants of this constitution partly resulted from the same crossings as those just described, the plants homozygous in green stigma also carrying one dose of short-style. The plants tested, therefore, are mostly the same as those given in Tables XXXI, XXXII and XXXIII.

The linkage found in diploids between **G** and **S** is, as the **GB** linkage, not very strong, a small difference existing between the male and female sides. Tables XXXIV and XXXV show that a similar low linkage exists in tetraploids.

Here again the agreement with expected numbers strongly favours the theory of an unchanged linkage value. The results of selfing the same plants (Table XXXVI) point in the same direction.

The agreement between actual and expected numbers is very striking.

Altogether the three cases of the genotype II (1) here studied all prove that crossing-over does take place in tetraploids between chromosomes coming from opposite parents; otherwise the **aB** class could not

TABLE XXXIV.

Case II (1). *Female back-crosses.*

$$\frac{GS}{gs}\,\frac{Gs}{gs} \times g_4s_4.$$

Family	No. of plants tested	GS	Gs	gS	gs
75–13	2	17	16	1	7
85–15	1	8	6	2	2
152–26	2	84	58	4	17
Total	5	109	80	7	26
Expected on a 2 : 1 basis		98·7	86·3	12·3	24·7
$M=$		7·4	6·5	3·4	4·7
Dev./$M=$		1·4	0·9	1·6	0·3

TABLE XXXV.

Case II (1). *Male back-crosses.*

$$g_4s_4 \times \frac{GS}{gs}\,\frac{Gs}{gs}.$$

Family	No. of plants tested	GS	Gs	gS	gs
56–14	1	12	20	5	7
85–15	1	8	9	—	—
152–26	2	35	39	1	6
Total	4	55	68	6	13
Expected on a 1·5 : 1 basis		52·9	64·8	8·1	16·2
$M=$		5·8	5·9	2·8	3·8
Dev./$M=$		0·4	0·5	0·7	0·8

TABLE XXXVI.

Case II (1). *Selfed plants.*

$$\frac{GS}{gs}\,\frac{Gs}{gs}\ \text{selfed.}$$

Family	No. of plants tested	GS	Gs	gS	gs
72–13	3	28	4	—	—
39–14	3	13	5	—	—
55–14	2	101	41	3	3
56–14	4	148	38	2	4
104–14	4	106	30	1	2
79*m*–15	1	21	8	—	—
85–15	2	21	10	—	—
152–26	1	23	8	1	1
Total	20	461	144	7	10
Expected		456·1	148·6	10·4	6·9
$M=$		11·0	10·6	3·4	2·6
Dev./$M=$		0·4	0·4	1·0	1·2

appear at all. Further, the distribution of the plants between the four classes makes it very likely that the percentage of crossing-over between these same chromosomes is the same in tetraploids as in diploids; this was particularly found to be the case for the linkages **B–G** and **B–S**.

Case II.

$$(2)\ \frac{\mathbf{Ab}}{\mathbf{aB}}\frac{\mathbf{Ab}}{\mathbf{ab}}.\ \text{Three dominants.}$$

The gametes formed by plants of this genotype are in a way reciprocal to the gametes formed in case II (1); the frequencies of the cross-over classes correspond to the non-cross-overs of the foregoing case and *vice versa*.

Pairing between chromosomes from opposite parents gives the following gametes:

$$\text{Non-cross-overs: } \mathbf{AB} + 2\mathbf{Ab} + \mathbf{aB},$$
$$\text{Cross-overs: } 2\mathbf{AB} + \mathbf{Ab} + \mathbf{ab}.$$

If, as before, the linkage is represented by the gametic ratio $x : 1$, we get from this kind of pairing the gametes

$$x\,(\mathbf{AB} + 2\mathbf{Ab} + \mathbf{aB}) + (2\mathbf{AB} + \mathbf{Ab} + \mathbf{ab}) = (x+2)\,\mathbf{AB} + (2x+1)\,\mathbf{Ab} + x\mathbf{aB} + \mathbf{ab}.$$

Again, pairing between chromosomes from same parents will result in the gametes $(x + 1)$ **AB** + $(x + 1)$ **Ab**, crossing-over, if such takes place, having no effect upon the final result.

The total amount of gametes formed in case II (2) is then expressed by

$$(2x+3)\,\mathbf{AB} + (3x+2)\,\mathbf{Ab} + x\mathbf{aB} + \mathbf{ab}.$$

Comparing this with the gametes formed in case II (1), we see that the only difference is that the frequencies of the classes **AB** and **aB** have been exchanged, and likewise the frequencies of the classes **aB** and **ab**.

Two different gene combinations of this type are present in the experiments.

1. $\frac{\mathbf{Bg}}{\mathbf{bG}}\frac{\mathbf{Bg}}{\mathbf{bg}}$. This genotype was obtained only once from a cross made by Gregory in 1914 between a plant homozygous in magenta flower colour and red stigma ($\mathbf{B_4g_4}$) and a plant homozygous in red flower colour and carrying only one dose of the gene **G** ($\mathbf{b_4G_1g_3}$). Plants from this cross having green stigma accordingly must be of the above type. Three plants from this cross were selfed, the results of which are given in Table XXXVII.

TABLE XXXVII.

Case II (2). *Selfed plants.*

$\frac{Bg}{bG}\frac{Bg}{bg}$ selfed.

Family	No. of plants tested	BG	Bg	bG	bg
95–15	3	94	40	3	1
Expected		100·1	34·1	3·4	0·4
	$M=$	5·3	5·1	1·8	0·6
	Dev./$M=$	1·2	1·2	0·2	1·0

There is a fairly good agreement between actual and expected numbers, supporting the theory that cross-over values between chromosomes from opposite parents in tetraploids are very near those found in diploids.

2. $\frac{Gs}{gS}\frac{Gs}{gs}$. Back-crosses and selfing of plants of this type have been made on a larger scale than those earlier described. The plants tested were made in the years 1922, 1923 and 1924 through crossings both ways between plants homozygous for red stigma and carrying one dose of short-style ($g_4S_1s_3$) and plants homozygous for green stigma and long-style (G_4s_4).

Female back-crosses are shown in Table XXXVIII, the results being, on the whole, slightly disappointing.

TABLE XXXVIII.

Case II (2). *Female back-crosses.*

$\frac{Gs}{gS}\frac{Gs}{gs}\times g_4s_4$.

Family	No. of plants tested	GS	Gs	gS	gs
102–23	4	66	89	10	14
103–23	1	26	26	8	1
105–23	1	17	18	3	3
114–24	4	121	86	27	15
116–24	1	8	10	2	2
144–25	3	37	27	4	5
145–25	1	6	12	2	1
150–25	4	105	105	26	19
155–25	3	46	59	17	8
Total	22	432	432	99	68
Expected on a 2 : 1 basis		400·9	458·2	114·6	57·3
	$M=$	15·6	15·9	10·1	7·4
	Dev./$M=$	2·0	1·6	1·5	1·4
Expected on a 1·5 : 1 basis		412·4	446·8	103·1	68·7
	$M=$	15·7	15·9	9·6	8·0
	Dev./$M=$	1·2	0·9	0·4	0·08

Although the numbers are comparatively high and the monofactorial distribution comes very near the expected ratios 5 : 1 and 1 : 1,

$$(\mathbf{G} : \mathbf{g} = 864 : 167, \ \mathbf{S} : \mathbf{s} = 531 : 500),$$

the agreement with expectation calculated on the basis of female linkage in diploids is not quite satisfactory. It is true that the deviations are less than three times the standard error, but even so the actual numbers seem to suggest a weakening of the linkage. Expected numbers, therefore, were calculated on a 1·5 : 1 basis, the gametic ratio found in diploids on the male side. The agreement between these numbers and those actually found is, as seen, striking. Whether this phenomenon is of real significance is difficult to decide. Probably small variations in linkage values appear here as in other material; in view of the result given in Table XXXIV this is the more probable explanation. The numbers, however, are of importance in showing that a low linkage exists on the female side corresponding to what is found in diploids.

The male back-crosses (Table XXXIX) are more satisfactory.

TABLE XXXIX.

Case II (2). *Male back-crosses.*

$$g_4s_4 \times \frac{\mathbf{Gs}}{\mathbf{gS}}\frac{\mathbf{Gs}}{\mathbf{gs}}.$$

Family	No. of plants tested	GS	Gs	gS	gs
102–23	3	12	13	3	1
105–23	1	6	15	2	3
114–24	1	17	11	5	2
Total	5	35	39	10	6
Expected on a 1·5 : 1 basis		36	39	9	6
$M=$		4·6	4·7	3·0	2·4
Dev./$M=$		0·2	0·0	0·3	0·0

Although the numbers here are small, there is a perfect agreement with what would be expected supposing that the linkage is the same as in diploids.

Selfing of the same plants further supports this theory (Table XL), a striking agreement existing between expected and actual numbers.

Summing up, the experiments covering different combinations of case III all show that crossing-over takes place between chromosomes coming from opposite parents, and that the percentage of crossing-over is probably for these genes the same as in diploids.

Case III.

$$(1)\ \frac{\mathbf{AB}}{\mathbf{ab}}\frac{\mathbf{ab}}{\mathbf{ab}}.\ \text{Two dominants.}$$

This arrangement of the genes is of great interest, because of the opportunity it offers of getting an answer to the question whether crossing-over takes place also between chromosomes coming from same parent. The experiments just related proved that an interchange of genes takes place between chromosomes coming from opposite parents, whereas they could tell nothing with regard to chromosomes coming from the same parent; as already repeatedly mentioned, crossing-over, if such takes place, will in the previous cases have no effect upon the final result.

Three alternatives present themselves:

1. Crossing-over takes place between chromosomes from same parent as well as between those from opposite parents and with equal frequency.

2. Crossing-over takes place *only* between chromosomes from opposite parents. No interchange between chromosomes from same parent.

TABLE XL.

Case II (2). *Selfed plants.*

$\frac{\mathbf{Gs}}{\mathbf{gS}}\frac{\mathbf{Gs}}{\mathbf{gs}}$ selfed.

Family	No. of plants tested	**GS**	**Gs**	**gS**	**gs**
102–23	1	51	13	3	—
114–24	4	89	39	2	—
116–24	1	4	4	—	—
144–25	3	162	50	1	1
145–25	1	38	12	1	—
150–25	4	250	76	9	3
155–25	3	159	36	6	—
Total	17	753	230	22	4
Expected		732·5	248·5	24·3	3·7
	$M=$	14·4	13·7	4·9	2·0
	Dev./$M=$	0·7	1·4	0·5	0·2

3. Crossing-over takes place between chromosomes coming from same parent, but at a different rate (linkage stronger or weaker) from that between chromosomes from opposite parents.

Between the four homologous chromosomes in question three different pairings will take place with equal frequency. The first alternative, crossing-over between any two of the four chromosomes, will from each of these pairings give the same gametes, namely $x\mathbf{AB} + \mathbf{Ab} + \mathbf{aB} + x\mathbf{ab}$, $x:1$ representing the gametic ratio found in diploids.

The second alternative, no crossing-over between chromosome coming from same parents, will, from two of the possible pairings, namely those between chromosomes from opposite parents, give these same gametes, while the third pairing, between chromosomes from same

parent, give only two kinds of gametes, the crossing-over classes missing. The results will be as follows:

(1)	x**AB** +	**Ab** +	**aB** +		x**ab**
(2)	x**AB** +	**Ab** +	**aB** +		x**ab**
(3)	$(x+1)$ **AB** +			+	$(x+1)$ **ab**
	$(3x+1)$ **AB** +	2**Ab** +	2**aB** +		$(3x+1)$ **ab**

This result will, in practice, give the impression of an increase in strength of linkage between the two genes as compared to diploids.

The third alternative, finally, will result in a gametic ratio depending upon the percentage of crossing-over between chromosomes from same parent. If the percentage of crossing-over is lower we get an apparent strengthening of the linkage, if it is higher we get an apparent weakening.

Only one genotype of this kind has so far been available:

$\frac{\mathbf{BS}}{\mathbf{bs}}\frac{\mathbf{bs}}{\mathbf{bs}}$. Plants of this type originated partly from crossings between plants carrying the two dominant genes and pure recessive plants, partly as offspring from selfed plants. In this last case their genotype has been ascertained only from what they gave when back-crossed.

Female back-crosses are given in Table XLI. The numbers expected,

TABLE XLI.

Case III (1). *Female back-crosses.*

$\frac{\mathbf{BS}}{\mathbf{bs}}\frac{\mathbf{bs}}{\mathbf{bs}} \times \mathbf{b_4s_4}$.

Family	No. of plants tested	BS	Bs	bS	bs
85–15	1	9	—	1	8
69–16	1	3	—	—	2
137–16	2	10	2	—	8
86–19	1	10	—	—	10
114–24	1	39	1	2	34
152–26	2	83	6	5	69
153–26	1	9	—	—	8
156–26	4	78	6	7	85
Total	13	241	15	15	224
Expected alternative (1)		236·6	19·4	18·1	220·9
$M=$		11·1	4·3	4·2	11·1
Dev./$M=$		0·4	1·0	0·7	0·3
Expected alternative (2)		243·1	12·9	12·1	226·9
$M=$		11·1	3·9	3·4	11·1
Dev./$M=$		0·2	0·5	0·9	0·3

according to the two first alternatives, together with their standard errors, are given. Because of the deficiency of reds and long-styles the calculation was made separately for magentas and reds.

As will be seen, it is not possible from these results to choose definitely between the two alternatives. The actual numbers agree about equally well with both alternatives, as appears from the ratio, deviation to standard error, in both cases. In diploids the amount of cross-overs between **B** and **S** is, on the female side, 7·5 per cent. In the case of alternative (2) there should be only about 5 per cent. of cross-overs. If we now calculate the percentage of cross-overs from the actual numbers we find 6·1 per cent., that is, a value intermediate between the two. This might indicate that crossing-over takes place also between chromosomes coming from same parent, but not so frequently as between those coming from opposite parents; the third alternative then would be the correct one. Apparently, however, a far greater number is required for definitely settling which alternative gives the correct solution.

Turning to the male back-crosses we meet with the same difficulties. Table XLII gives the numbers obtained, together with the expected numbers.

TABLE XLII.

Case III (1). *Male back-crosses.*

$$\mathbf{b_4 s_4} \times \frac{\mathbf{BS}\ \mathbf{bs}}{\mathbf{bs}\ \mathbf{bs}}.$$

Family	No. of plants tested	**BS**	**Bs**	**bS**	**bs**
56–14	1	13	2	4	25
85–15	1	8	2	—	8
69–16	4	19	1	2	18
137–16	5	27	—	2	24
56–16	1	18	—	—	18
114–24	1	8	—	—	5
152–26	2	32	5	4	30
153–26	2	13	2	—	13
Total	17	138	12	12	141
Expected alternative (1)		132·6	18·9	18·9	132·6
$M=$		8·6	4·2	4·2	8·6
Dev./$M=$		0·6	1·6	1·6	1·0
Expected alternative (2)		138·9	12·6	12·6	138·9
$M=$		8·7	3·5	3·5	8·7
Dev./$M=$		0·1	0·2	0·2	0·3

Again, both alternatives are possible, although the second one in this case seems to be more in agreement with the actual numbers. In diploids the male linkage is expressed by the gametic ratio 7 : 1, or 12·5 per cent. of cross-overs. Alternative (2) would give an apparent change of the cross-over percentage to 8·2. The actual numbers in Table XLII give a cross-over percentage of 7·9, a result which goes in favour of the second alternative.

Summing up, one must admit that both tables may be interpreted in different ways. Both kinds of back-crosses, however, suggest that as regards the piece carrying the genes **B** and **S**, little or no interchange takes place between the chromosomes coming from same parent.

Another explanation would be to suppose a general strengthening of the linkage in tetraploids. But this suggestion is not supported by the result earlier reported (see Table XXX).

Case III.

$$(2)\ \frac{\mathbf{Ab}}{\mathbf{ab}}\,\frac{\mathbf{aB}}{\mathbf{ab}}.\ \text{Two dominants.}$$

Further information concerning the questions discussed above should be obtainable from this arrangement of the genes. A theoretical consideration will show that in this case one ought to have a far better chance of arriving at a definite conclusion.

Again there are three possible ways of pairing between the four chromosomes in question. Pairing between chromosomes from opposite parents will here give all four classes of gametes in equal numbers; crossing-over, if such takes place, can have no visible effect upon the gametic ratio. The crucial pairing will, in this case, be the one between chromosomes from same parent. In case of no crossing-over as before only two classes of gametes are found, whereas otherwise four classes will appear.

Let us again consider the three alternatives dealt with in case III (1).

1. Crossing-over takes place between any two of the four homologous chromosomes, regardless of which way they entered the plant.

If the strength of the linkage is expressed by the gametic ratio $1 : x$, the three possible pairings of the chromosomes will result in the following gametes:

$$\begin{array}{lllll}
(1) & (x+1)\,\mathbf{AB} + & (x+1)\,\mathbf{Ab} + & (x+1)\,\mathbf{aB} + & (x+1)\,\mathbf{ab} \\
(2) & (x+1)\,\mathbf{AB} + & (x+1)\,\mathbf{Ab} + & (x+1)\,\mathbf{aB} + & (x+1)\,\mathbf{ab} \\
(3) & 2\mathbf{AB} + & 2x\mathbf{Ab} + & 2x\mathbf{aB} + & 2\mathbf{ab} \\
\hline
 & (x+2)\,\mathbf{AB} + & (2x+1)\,\mathbf{Ab} + & (2x+1)\,\mathbf{aB} + & (x+2)\,\mathbf{ab}
\end{array}$$

(1) and (2) represent, as before, pairings of chromosomes from opposite parents, (3) pairings of chromosomes from same parent. The total number of gametes is in each of the three cases $4x + 4$. Back-crossings will, in this case, give an apparent lowering of the linkage value.

2. Crossing-over only between chromosomes from opposite parents.

The formation of gametes will here take place according to the following scheme:

$$\begin{array}{ll} (1) & \mathbf{AB} + \mathbf{Ab} + \mathbf{aB} + \mathbf{ab} \\ (2) & \mathbf{AB} + \mathbf{Ab} + \mathbf{aB} + \mathbf{ab} \\ (3) & \quad 2\mathbf{Ab} + 2\mathbf{aB} \\ \hline & \mathbf{AB} + 2\mathbf{Ab} + 2\mathbf{aB} + \mathbf{ab} \end{array}$$

In this case the effect of linkage has been completely eliminated. Regardless of the strength of the linkage between the two genes, the two middle classes will always be twice as big as the outer classes.

Owing to this striking phenomenon it ought to be easy to decide between alternatives (1) and (2) or more correctly to decide whether crossing-over takes place between the chromosomes coming from same parent or not. The difference between the two alternatives is most pronounced for small linkages. The stronger the linkage the more the two alternatives will approach each other, the range of variation being between near equality and the ratio 1 : 2 between the classes.

From these considerations we may once more turn to the experiments.

The above genotype was produced by crossing plants carrying both dominants with double recessives. It is not possible to tell beforehand whether the dominant genes will be in the same or in separate chromosomes. Even if the genes entered the P_1 plants from different sides their arrangements might easily be changed by crossing-over. The genotypes III (1) and III (2) are, however, easily distinguishable from back-crosses.

No plant of the type containing **B** and **S** together has been obtained. The reason for this is that these genes originally entered the experiments in the same chromosome; with a comparatively strong linkage like this there is only a small chance of getting the genotype wanted. This is, however, of small importance because, as already mentioned, the stronger the linkage the more difficult it is to distinguish between the two alternatives.

$\frac{\mathbf{Gb}}{\mathbf{gb}}\frac{\mathbf{gB}}{\mathbf{gb}}$. Male and female back-crosses. Plants of this type are given in Tables XLIII and XLIV.

The high crossing-over percentage existing between these two genes makes this combination an excellent opportunity for judging between the different alternatives, *i.e.* for deciding whether crossing-over takes place between chromosomes coming from the same parent or not.

In Table XLIII there is an excess of plants with green stigma. In calculating the expected numbers, therefore, plants with green and red

stigmas have been treated separately. The table proves convincingly that crossing-over has taken place between the chromosomes **Gb** and **gB**; otherwise the middle classes would have been twice as numerous as the outer classes. Moreover, the agreement with expected numbers is very striking, indicating that the linkage value is of the same order in tetraploids as in diploids.

TABLE XLIII.

Case III (2). *Female back-crosses.*

$$\frac{\mathbf{Gb}}{\mathbf{gb}}\frac{\mathbf{gB}}{\mathbf{gb}} \times \mathbf{g_4b_4}.$$

Family	No. of plants tested	GB	Gb	gB	gb
95–15	1	4	3	4	4
153–26	1	4	5	5	3
156–26	4	39	57	46	35
Total	6	47	65	55	42
Expected on a 2·2 : 1 basis		49·0	63·0	54·6	42·4
	$M=$	6·0	6·6	6·6	5·6
	Dev./$M=$	0·3	0·3	0·1	0·1

TABLE XLIV.

Case III (2). *Male back-crosses.*

$$\mathbf{g_4b_4} \times \frac{\mathbf{Gb}}{\mathbf{gb}}\frac{\mathbf{gB}}{\mathbf{gb}}.$$

Family	No. of plants tested	GB	Gb	gB	gb
56–16	1	9	8	8	10
153–26	1	4	7	6	3
156–26	1	3	2	2	1
Total	3	16	17	16	14
Expected on a 1·9 : 1 basis		14·1	17·4	17·4	14·1
	$M=$	3·3	3·5	3·5	3·3
	Dev./$M=$	0·6	0·1	0·4	0·0

The male back-crosses, although presenting very small numbers, strongly support the above conclusion, both as regards an interchange between chromosomes from the same parent, and the stability of the crossing-over value.

$\frac{\mathbf{Gs}}{\mathbf{gs}}\frac{\mathbf{gS}}{\mathbf{gs}}$. As in the foregoing case, we are here dealing with a low linkage, green stigma (**G**) and short-style (**S**) lying even further apart than **B** and **S**. Back-crossing plants of this type leads to the same result. Apparently crossing-over takes place between chromosomes from the same parent, and the linkage value must be somewhere near, or the same as that found in diploids.

Altogether these last experiments (case III (2)) prove that, as regards the linkages **B–G** and **G–S**, crossing-over takes place between chromosomes originating from the same parent. The experiments also point to a stability in the crossing-over value.

TABLE XLV.

Case III (2). *Female back-crosses.*

$$\frac{\mathbf{Gs}}{\mathbf{gs}}\frac{\mathbf{gS}}{\mathbf{gs}} \times g_4s_4.$$

Family	No. of plants tested	GS	Gs	gS	gs
153–26	1	4	5	5	3
156–26	4	41	55	45	36
Total	5	45	60	50	39
Expected on a 2 : 1 basis		46·7	58·3	49·5	39·5
$M=$		5·9	6·4	6·1	5·6
Dev./$M=$		0·3	0·3	0·1	0·1

TABLE XLVI.

Case III (2). *Male back-crosses.*

$$g_4s_4 \times \frac{\mathbf{Gs}}{\mathbf{gs}}\frac{\mathbf{gS}}{\mathbf{gs}}.$$

Family	No. of plants tested	GS	Gs	gS	gs
56–16	1	9	8	9	10
153–26	1	3	8	5	4
156–26	1	3	2	2	1
Total	3	15	18	16	15
Expected on a 1·5 : 1 basis		14·9	17·1	17·1	14·9
$M=$		3·4	3·5	3·5	3·4
Dev./$M=$		0·0	0·3	0·3	0·0

Double crossing-over.

In some of the experiments related above all three genes **S**, **B** and **G** were involved. From these cases I have tried to solve the question of double cross-over in tetraploids. Obviously three pairs of genes may be distributed among four homologous chromosomes in a great many different ways, the situation being far more complicated than when only two pairs of genes are present. I have thought it unnecessary to enter into a discussion of all the different possibilities, because only a very few of them are present in these experiments. Actually only one of them proved to be of any interest, and this alone will be treated in detail.

The order of the three genes in question is (**S–B–G**) in the chromosomes of a diploid plant, the distance **S–B** being, as mentioned before, comparatively short (7 or 12 per cent.), while the **B–G** distance is longer (*ca.* 33 per cent.). The only object of the following analysis has been to

examine whether double cross-over happens in tetraploids or not. The material is, at present, far too small for solving questions such as interference, or other problems in connection with double cross-over.

$\frac{\mathbf{SBG}}{\mathbf{sbg}}\ \frac{\mathbf{sbG}}{\mathbf{sbg}}$. Plants of this genotype, which is present in some of the experiments, will form gametes after the following scheme.

Pairing between chromosomes from opposite parents will give:

	Non-cross-overs		0–1		1–2		0–1–2	
	SBG	**sbg**	**Sbg**	**sBG**	**SBg**	**sbG**	**SbG**	**sBg**
sbG	**SBG**	**sbG**	**SbG**	**sBG**	**SBG**	**sbG**	**SbG**	**sBG**
sbg	**SBG**	**sbg**	**Sbg**	**sBG**	**SBg**	**sbG**	**SbG**	**sBg**

denoting the loci of **S**, **B** and **G** respectively as 0, 1 and 2.

That is, gametes:

SBG. Consisting of 2 non-cross-over classes + 1 (1–2) cross-over class.
sbg. A pure non-cross-over class.
Sbg. A pure 0–1 cross-over class.
sBG. 2 (0–1) + (0–1–2).
SBg. A pure 1–2 cross-over class.
sbG. 1 non-cross-over class + 2 (1–2) cross-over classes.
SbG. (0–1) + 2 (0–1–2).
sBg. A pure 0–1–2 double cross-over class.

Pairing between chromosomes from the same parent will give:

Non-cross-overs		0–1		1–2		0–1–2	
SBG	**sbG**	**SbG**	**sBG**	**SBG**	**sbG**	**SbG**	**sBG**

that is:

SBG. Consisting of 1 non-cross-over class + 1 (1–2) cross-over class.
sBG. (0–1) + (0–1–2).
sbG. 1 non-cross-over class + 1 (1–2) cross-over class.
SbG. (0–1) + (0–1–2).

The other four classes are here missing. We see that, in this case, 1–2 cross-overs are not distinguishable from non-cross-overs, and double cross-overs cannot be distinguished from 0–1 cross-overs.

If these are added to the foregoing we get the classes of gametes consisting of:

SBG. 3 non-cross-over classes + 2 (1–2) cross-over classes.
sbg. *A pure non-cross-over class.*
Sbg. *A pure* 0–1 *cross-over class.*
sBG. 3 (0–1) + 2 (0–1–2).
SBg. *A pure* 1–2 *cross-over class.*
sbG. 2 non-cross-over classes + 3 (1–2) cross-over classes.
SbG. 2 (0–1) + 3 (0–1–2).
sBg. *A pure* 0–1–2 *double cross-over class.*

Table XLVII shows the numbers obtained from back-crossing plants of this type. Male and female sides have not been separated.

TABLE XLVII.

Male and female back-crosses from plants of the above genotype, showing the existence of double cross-over in tetraploids.

$\frac{\mathbf{SBG}}{\mathbf{sbg}}\,\frac{\mathbf{sbG}}{\mathbf{sbg}}$ back-crossed.

Family	No. of plants tested	Non-cross-overs		0–1		1–2		0–1–2	
		SBG	**sbg**	**Sbg**	**sBG**	**sbG**	**SBg**	**SbG**	**sBg**
56–14	1	10	7	2	2	18	3	2	—
185–15	1	16	2	1	2	14	1	—	—
152–26	2	110	22	—	10	77	5	9	1
Total	4	136	31	3	14	109	9	11	1
Expected		111	31	3	11	89	9	9	1

First of all we note that one important plant of the class **sBg** has appeared. The **sBg** class is a pure double cross-over class; this one plant therefore proves that a double cross-over has taken place between chromosomes coming from opposite parents. It happens that this is the only plant in the whole material of this kind.

Calculation of expected numbers has, in this case, been based upon the theoretically pure classes, **sbg**, **Sbg**, **SBg** and **sBg**. Assuming that these classes come approximately correct the other classes have then been calculated after the scheme given above. Table XLVII shows that the compound classes **SBG**, **sBG**, **sbG** and **SbG** came fairly near to expectation; the excess of **G** accounts for the discrepancy in expectation for **SBG** and **sbG**, the ratio **G** : **g** being nearly 6 : 1 instead of 5 : 1.

Two more cases with plants containing all three genes were present in the experiments. One was a plant of the genotype $\frac{\mathbf{SBg}}{\mathbf{sbg}}\,\frac{\mathbf{sbG}}{\mathbf{sbg}}$; in this case all the classes of gametes will, however, be of compound nature and, therefore, not of much interest. The second case, of the genotype $\frac{\mathbf{SBg}}{\mathbf{sbG}}\,\frac{\mathbf{sBg}}{\mathbf{sbG}}$, one of the double cross-over classes, ought to come pure; this class did not, however, appear among the relative few numbers obtained from back-crossing, and I have, therefore, not thought it worth while to analyse this case before greater numbers are available.

These experiments on linkage in a tetraploid plant have led to the result that an interchange may take place between all the four homologous chromosomes, both between those coming from opposite parents

and between those coming from the same parent. Further, it was found that double crossing-over may occur between chromosomes coming from opposite parents; more data are wanted for elucidating the question whether double crossing-over may also occur between chromosomes from the same parent.

The results here arrived at agree with what is found in triploid races of *Drosophila melanogaster*. L. V. Morgan (1925) finds that, in triploid females having two attached X-chromosomes, crossing-over may take place between the attached X's and the free X; further, that crossing-over also takes place between the attached X's *inter se*, *i.e.* between chromosomes coming from the same parent.

Bridges (1925) arrived at similar conclusions from a study of triploid females with unattached X's. Here, again, crossing-over may take place between any two of the three chromosomes. Double cross-overs also took place, and he further succeeded in proving that crossing-over can take place simultaneously between all three chromosomes; that is, one cross-over may take place between two chromosomes, while at the same time a second cross-over may take place between one of these and the third chromosome. This he thinks proves that synapsis generally involves all three X's. In *Primula* this point wants further investigation; at present cytological evidence, as will be shown presently, appears not to contradict such a supposition. Concerning the percentage of crossing-over Bridges finds in his triploid race that, in one part of the X-chromosomes, the percentage of crossing-over is twice as high as in the diploid controls, while in another part of the chromosomes it is only one-half as high.

Another point of interest is that these experiments on linkage in a tetraploid form give a second and conclusive proof that the four homologous chromosomes pair at random, regardless of the way in which they entered the plants. This evidence then supports the conclusion previously drawn from the ratios appearing in F_2's and back-crosses from monofactorial crossings.

Cytology.

P. sinensis, and especially its tetraploid form, is not a favourable object for cytological investigation. The chromosomes are small and crowded, and the material does not easily lend itself to fixation. Different methods of fixation were tried, among them strong and weak Flemming and Carnoy's fluid. The best result was obtained by using the modified Flemming solution (60 c.c. 1 per cent. chromic acid, 20 c.c. 2 per cent.

osmic acid and 25 c.c. 10 per cent. acetic acid) introduced by the late W. C. F. Newton, to whom I am greatly indebted for help and advice. The sections were then stained in gentian violet after the method of Newton (Newton and Darlington, 1929). The meiotic stages reproduced on Plate XXIV have all been treated in this way.

In the following, some of the main features of pollen maturation are given. I am hoping in a later communication to give a more detailed description of the process. Great stress was laid upon getting clear pictures from the diakinetic stages, because, from analogy with other tetraploids, it was expected that these would demonstrate the existence of the sets of four homologous chromosomes predicted through the genetical experiments. It was soon found that diakinetic and metaphase stages from the first maturation division were scarce. These stages are apparently passed through quickly, while early prophase and pollen tetrads are frequently found. The second maturation division also appears to last longer and is more easily fixed.

As already stated, the diploid form of *P. sinensis* has in its somatic cells 12 pairs of chromosomes, while the tetraploid variety has 48 chromosomes, or 12 sets of four homologous chromosomes. The genetical experiments related above prove that, as regards five of these sets at any rate, the four homologous chromosomes are distributed at random during the maturation divisions. The question arises whether conjugation in tetraploids of this kind takes place in pairs, or whether all four chromosomes unite during early prophase.

Cases supporting this last hypothesis were mentioned in the foregoing section. L. V. Morgan (1925) and Bridges (1925) succeeded in proving that in triploid *Drosophila* crossing-over may take place simultaneously between all three chromosomes; according to the present conception of the mechanism of crossing-over this implies pairing of the three chromosomes during prophase. Cytological evidence is given by Newton (1929); in triploid tulips he found that during prophase three threads lie side by side; only pairs of homologous chromosomes were found to associate at any particular point, but different pairs associate at different points; the possibility of a simultaneous crossing-over is thus afforded. In diakinesis all three corresponding chromosomes are either found as trivalents, or one of them may come to lie entirely free. Similar conditions were found by Darlington (1929) in triploid and tetraploid hyacinths. Polyploid tulips and hyacinths are, however, of unknown origin, and some caution must, therefore, be used when paralleling these cases with those of *Drosophila* and *Primula*.

The present material is not good enough for solving the question of pairing during early prophase. But the arrangement of the chromosomes at diakinesis may give some clue to the answer. Belling and Blakeslee (1924) claim to have found that in the tetraploid *P. sinensis* "if several hundred well-fixed first metaphases are examined, and compared with those of the diploid form, it seems as if the majority of the 48 chromosomes were usually arranged in sets of two pairs each and rarely twelve such sets may be counted." My experience does not agree with this statement. Pollen mother cells in diakinesis from tetraploid *Primula* are shown in Plate XXIV, figs. 1–5. As seen, quadrivalents are found in most of the cells, but as a rule not more than one or two in any one cell. More seldom three or four such arrangements may be recognised in one cell. The majority of the chromosomes are arranged in bivalents. The mixture of quadrivalents and bivalents may be seen from the figures. An arrangement of the chromosomes in even approximately twelve sets was never found.

The four chromosomes constituting a quadrivalent can be arranged in different ways. Most commonly found are figures of eight, but open or oval rings may also be found, or the four chromosomes may lie side by side after each other (as in Plate XXIV, fig. 9). Some of these configurations are shown under higher magnification in Plate XXIV, figs. 6–11.

In other tetraploids similar quadrivalents have been demonstrated. Thus, in tetraploid *Datura*, whose origin is probably analogous to that of the tetraploid *Primula*, Belling and Blakeslee (1924) found that "at the late prophase and the metaphase of the first division in the pollen mother cells, the chromosomes are as a rule arranged in connected sets of four each."

In the tetraploid *Solanum nigrum* and *S. lycopersicum*, experimentally produced and examined by Jörgensen (1928), it appears that conjugation of the chromosomes is in most cases normal, but in many of the nuclei a few tetrasomes are present, generally arranged in rings or figures of eight.

It was stated above that, among polyploids of unknown origin, one or a few trivalents and quadrivalents are often found in pollen mother cells at diakinesis. Such arrangements were found by Newton and Darlington (1929) in tulips and hyacinths; in these cases association during early prophase was also demonstrated. From these extremely beautiful and accurate cytological investigations one may venture to draw a parallel, and advance the hypothesis that when quadrivalents are found at diakinesis very likely association of all four chromosomes may happen at early prophase.

Following upon diakinesis the chromosomes arrange themselves on the spindle. It is doubtful whether the quadruple condition is maintained during this stage; most likely the chromosomes are now arranged in pairs; the chromosomes on the equatorial plates of the first maturation division are in the tetraploid *Primula* too crowded for reliable counts; but more than 20 chromosomes may nearly always be counted and the chromosomes are of very even size, which would not be expected if some of them were of tetrasomic origin. Another phenomenon was observed during this stage; in some of the cells undivided chromosomes could be seen to go towards one of the poles, while the rest of the chromosomes were still arranged in the equatorial plate. An example of this is shown in Plate XXIV, fig. 12, which gives three adjoining cells, two of which are normal, while in the third an undivided chromosome is seen to go towards one of the poles.

The second maturation division follows immediately upon the first. Owing to the smaller size the chromosomes are here easier to count. Plate XXIV, fig. 13 shows a plate containing the normal number of 24 chromosomes. As in the first division non-disjunction of chromosomes is frequently met with. In Plate XXIV, fig. 14 a group of three is seen to go towards one of the poles. These irregularities, met with in both maturation divisions, must result in an unequal distribution of the chromosomes among the pollen tetrads. The equatorial plate given in Plate XXIV, fig. 14 contains only 21 chromosomes; equatorial plates with less than 24 chromosomes are, on the whole, frequently found; plates with more than 24 chromosomes have so far not been identified; but many plates are difficult to count, and the non-existence of plates with too many chromosomes cannot be said to be proved. It has been mentioned earlier that the pollen tetrads formed in the tetraploid *P. sinensis* are very regular; in spite of that they will, as the foregoing shows, contain a varying number of chromosomes, and this may be one of the reasons for the lowered fertility of these plants.

Non-disjunction of chromosomes during maturation division is reported by Belling and Blakeslee (1924) to be a regular phenomenon in tetraploid *Datura*; they found that the amount of 23 + 25 chromosome distribution after reduction division averaged 25 per cent.

Another phenomenon met with in the second division of tetraploid *Primula* is the formation of giant cells. One of these is pictured in Plate XXIV, fig. 15; the exact number of chromosomes in this cell is difficult to settle; it seems, however, to lie between 44 and 48; obviously these giant cells originate from the fusion of two spindles. How such a

fusion comes about is illustrated in Plate XXIV, figs. 16 and 17; fig. 17 shows two spindles of the second maturation division in parallel position; in fig. 16 a giant cell is formed, and the two equatorial plates from which it originated may still be recognised. What happens to these tetraploid gametes is so far unknown; possibly they form the giant pollen grains described on p. 454. Similar fused plates are described by Jörgensen (1928) in an artificially produced triploid form of *Solanum nigrum*.

For comparison the diakinesis and metaphase of the maturation division in a diploid plant of *P. sinensis* is given in Plate XXIV, figs. 18–22. The cells are seen to be only about half the size, and the chromosomes form during diakinesis regular bivalents. The equatorial plates of the first division are very regular, and the 12 chromosomes are easily counted.

TETRAPLOIDY AS A FACTOR IN EVOLUTION.

Tetraploid and polyploid forms have, in recent years, been subject to extensive cytological studies, and these, in connection with the growing knowledge on chromosomes numbers in related species, have left small doubt as to the significance of chromosome doubling as a factor in evolution. The importance of polyploidy for the formation of new species has lately been discussed in detail by several authors (Jörgensen, 1928; Heilborn, 1922; Darlington, 1929, and others); I shall, therefore, here restrict myself to a brief mention of the main facts together with a discussion of problems specially connected with the present material.

It is well known that, in several cases, related species may be arranged in arithemetical series according to their chromosome numbers; a list of chromosome numbers may be found in Harvey (1920) and Tischler (1927) for animals and plants respectively. The phenomenon appears to be more commonly found in plants than in animals and, according to a hypothesis advanced by Muller (1925), this is due to the difficulty of establishing tetraploidy in forms with two sexes; in animals this is the more common type of propagation, while most of the higher plants are hermaphroditic.

Chromosome series of this kind at once suggest doubling of chromosomes as a possible step towards the formation of new species. Certain phenomena met with in meiosis of several of these polyploid forms indicate that this doubling is due to a longitudinal splitting of chromosomes, comparable to what we have found in *P. sinensis*; we may recall the facts mentioned earlier, that in several cases multiple associations of the chromosomes, as for instance trivalents and quadrivalents, are found

during diakinesis corresponding to similar arrangements found in tetraploids of known origin.

The objection may be raised that, in no case where doubling of chromosomes has taken place under control, has this process resulted in the formation of a new species. The tetraploid variety of *P. sinensis* forms no exception to this. It could, however, hardly be expected that a mere doubling of chromosomes should produce a new gene complex, which is a necessary qualification for a new species. The importance of the doubling more likely lies in the opportunities it gives for increasing the number of new genes. In the case of *P. sinensis* one criterion of a new species is, however, fulfilled; a new variety has appeared which shows practically complete incompatibility to the variety from which it arose; and if a cross is obtained the hybrid is absolutely self-sterile. In order to establish a new species it is necessary that the new genes appear, and further that some change takes place in the chromosomes so that a random assortment of the four chromosomes is no longer possible; the tetraploid then will behave genetically as a new diploid species.

There are certain phenomena met with in genetics which suggest that the process outlined above is just what has happened within certain species. I am referring to the phenomenon described as *multiple factors*. If, in the case here studied, a change took place in the chromosomes so that chromosomes from opposite parents could only go to opposite poles at the reduction division, we should no longer, for the genes studied, expect the 35 : 1 F_2 ratio and a 5 : 1 ratio from back-crosses; the corresponding ratios would now be 15 : 1 in F_2 and 3 : 1 in back-crosses. We have already seen that these were the ratios naturally expected by Gregory (1914). To a geneticist there is at once something very familiar about these ratios, they are, in fact, the ratios known from cases of two pairs of multiple or cumulative factors.

Among the best known cases of multiple factors are those described by Nilsson-Ehle (1909) in wheat. Cytological studies in wheat (Kihara, 1924; Watkins, 1924–9, and others) have now revealed some very interesting facts. The ordinary edible wheat, *Triticum vulgare*, is a hexaploid form. In *Triticum* three groups have been described, a diploid, a tetraploid and a hexaploid, the haploid number of chromosomes being 7, 14 and 21 respectively. *T. vulgare* is supposed to have its origin in a cross between a diploid and a tetraploid species; the result would be a triploid plant which, through doubling of its chromosomes, again would give the numbers actually found. If this is true, doubling of chromosomes has taken place twice in the evolution of common wheat, first a simple

doubling like that described in *P. sinensis*, and next a species-crossing followed by doubling of the chromosomes such as is found in *P. Kewensis*. The appearance of multiple factors could easily be accounted for by this process.

It is a question whether all cases of real multiple factors, not to be confused with modifying factors, are not due to doubling of chromosomes and thereby of genes in one of the ancestors of the species, with lower chromosome number.

Summary.

1. The present investigation deals with the tetraploid form of *P. sinensis*, its genetics and cytology, together with some observations concerning its fertility and cross-fertility to the diploid form from which it arose.

2. Tetraploid plants of *P. sinensis* arise spontaneously in diploid families. The doubling of the chromosomes is most likely due to a suspended mitosis at the first, or at one of the first divisions of the fertilised egg.

3. The fertility of tetraploids is considerably lowered; more flowers fail to set, and the average number of seeds per capsule is smaller than in diploids. The lowered fertility was found to be partly due to the incompatibility of the illegitimate cross, long × long, a combination which happened to be frequently used in the experiments. Another factor influencing the fertility of the plants seems to be the smaller power of germination of the pollen grains of tetraploids; this may be due to an uneven distribution of the chromosomes during maturation divisions, as demonstrated in the cytological part.

4. The cross, tetraploid × diploid, or *vice versa*, proved to be almost completely sterile. During the whole investigation only three triploid plants were obtained, although several hundred crosses were tried each year. All three triploid plants proved to be completely self-sterile. One plant was, however, obtained from the cross, triploid × diploid, and one plant from the cross, tetraploid × triploid, the number of chromosomes in these plants being 26 and 47 respectively. In each successful cross the higher number of chromosomes entered from the female side.

5. The genetical experiments included seven different genes, all well known in the diploid form, and also known to be distributed among five different pairs of chromosomes. The main object of the experiments was to settle the question of a random or selected assortment of the four homologous chromosomes present in a tetraploid plant of this kind. In

six of the cases studied, including four pairs of chromosomes, plants of the constitution $\mathbf{A}_2\mathbf{a}_2$ were found to give a 35 : 1 F_2 ratio and a ratio of 5 : 1 in back-crosses, thus strongly supporting the theory that conjugation takes place between the four chromosomes at random.

Another object was to study the quantitative effect of the genes when present in different doses. Only two of the genes studied showed complete dominance, that is, one dose of the dominant gene proved sufficient for the manifestation of the character in question. As regards four other genes, the $\mathbf{A}_1\mathbf{a}_3$ heterozygotes were found to be intermediate and mostly strongly variable. The seventh gene (**Ch**) proved so variable in its manifestation as to make classification impossible, and it was accordingly excluded from the experiments.

One of the genes studied, that for "Primrose Queen" eye (**q**), proved to be of special interest. The gene affects two different parts of the flower, namely, the size of the "eye" and the shape of the pistil. It was found that, whereas four doses of **q** are necessary to produce the big eye, three doses are sufficient to change the shape of the pistil.

6. In the diploid form three of the genes here studied lie in the same chromosome. These genes were found to be linked in tetraploids as well. Experiments with plants containing these genes in different arrangements elucidated the fact that crossing-over may take place between any two of the four chromosomes, both between chromosomes coming from opposite parents and between chromosomes coming from the same parent. One case of double cross-over was found, the interchange in this case having taken place between chromosomes from opposite parents.

7. Cytological studies revealed that during diakinesis some of the sets of four homologous chromosomes may be arranged in quadrivalents. Mostly only one or two such quadrivalents are present in any one pollen mother cell, the rest of the chromosomes being arranged in bivalents. Twelve quadrivalents were never found in any cell.

Non-disjunction of chromosomes was found to occur during both maturation divisions. Giant cells were found to appear in the second division.

8. A short discussion is given on the significance of tetraploidy in evolution, and the possible connection between doubling of chromosomes and multiple factors.

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EXPLANATION OF PLATES XIX—XXIV.

Plate XIX.

Triploid plant from the cross "moss-curl" (tetraploid) × magenta, green stigma, short-style (diploid). The plant was magenta, green stigma, long-style, the diploid plant being heterozygous in *S*.

Plate XX.

Fig. 1. Red, green stigma, short-style ($\mathbf{w_4G_4}$).

Fig. 2. Flower with reddish tinge, green stigma, long-style, and 7 petals ($\mathbf{w_4G_4}$).

Fig. 3. Red, red stigma, short-style ($\mathbf{w_4g_4}$).

Fig. 4. Magenta lavender, green stigma, long-style ($\mathbf{W_1w_3}$).

Fig. 5. Tinged white with magenta flush, red stigma, long-style ($\mathbf{W_2w_2g_4}$).

Fig. 6. Pink lavender, green stigma, long-style ($\mathbf{W_1w_3}$).

Fig. 7. Red lavender, red stigma, long-style ($\mathbf{W_1w_3g_4}$).

All the flowers natural size.

Plate XXI.

Fig. 1. Tetraploid flower with large eye ("Primrose Queen") and *sinensis* shape ($\mathbf{q_4}$). Natural size.

Fig. 2. Calyx from flower off the same plant as fig. 1, showing the characteristic shape of the stigma connected with the large eye ($\mathbf{q_4}$). $\times 1\frac{1}{3}$.

Fig. 3. Calyx and stigma from a large-eyed plant with *stellata* flower. The style slightly longer ($\mathbf{q_4}$). $\times 1\frac{1}{3}$.

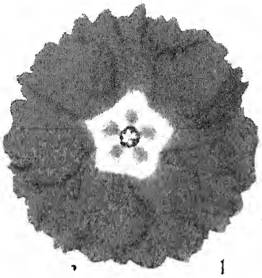
Fig. 4. Homostyled flower with normal eye ($\mathbf{Q_1q_3}$). Natural size.

Fig. 5. Side-view of flower from the same plant as fig. 4, showing the position of the anthers. Natural size.

Fig. 6. Calyx and style of a normal long-styled flower ($\mathbf{Q_4}$). $\times 1\frac{1}{3}$.

Fig. 7. Style and stigma of homostyled flower ($\mathbf{Q_1q_3}$). $\times 1\frac{1}{3}$.

Fig. 8. Stigma of the heterozygous type ($\mathbf{Q_2q_2}$). $\times 1\frac{1}{3}$.



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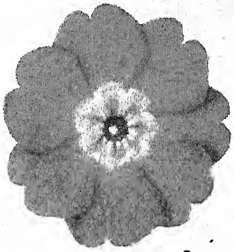

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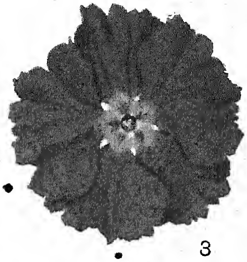

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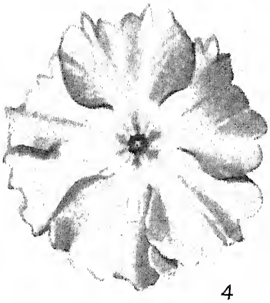

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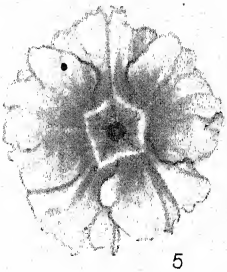

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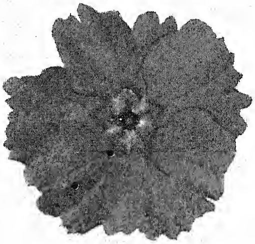

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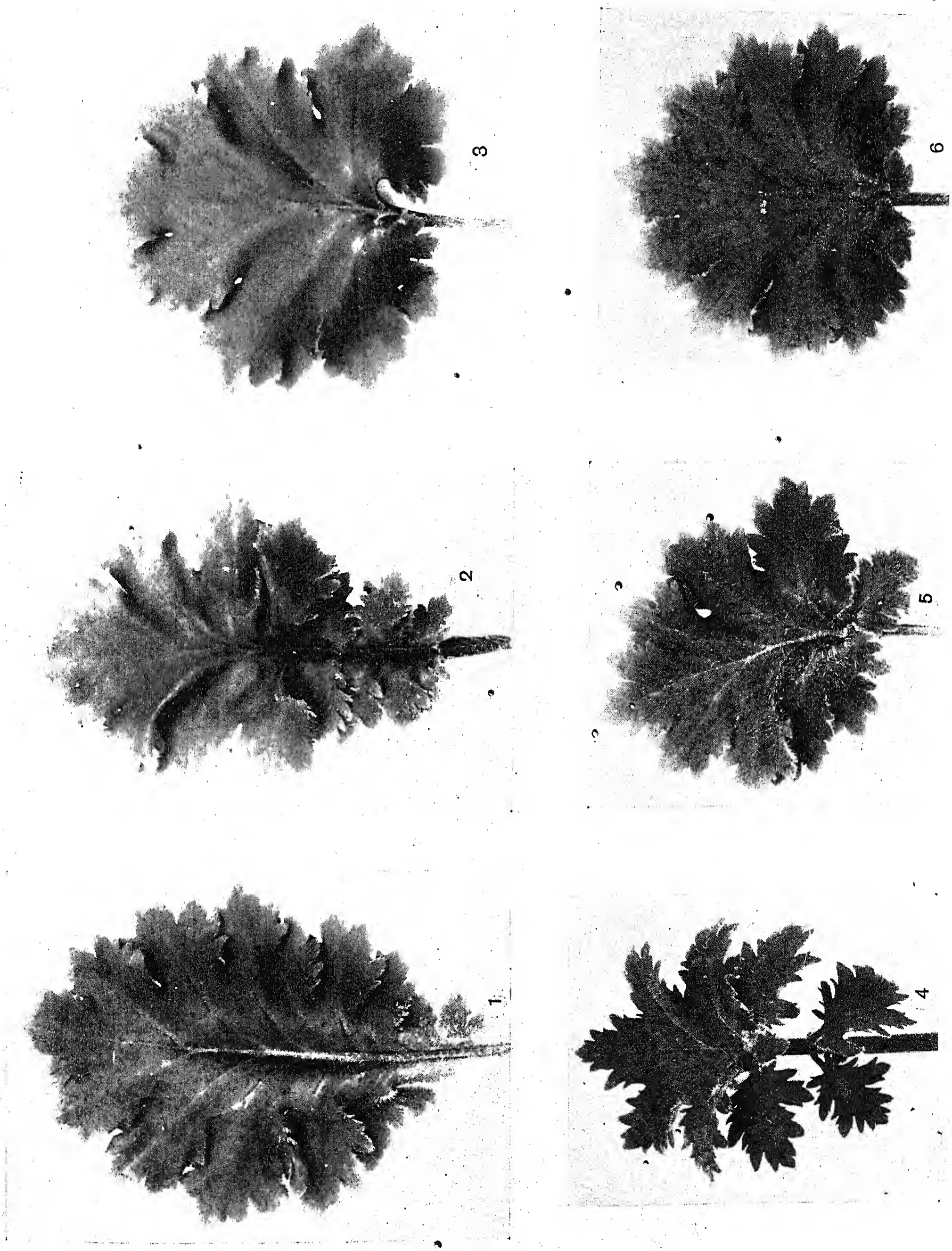
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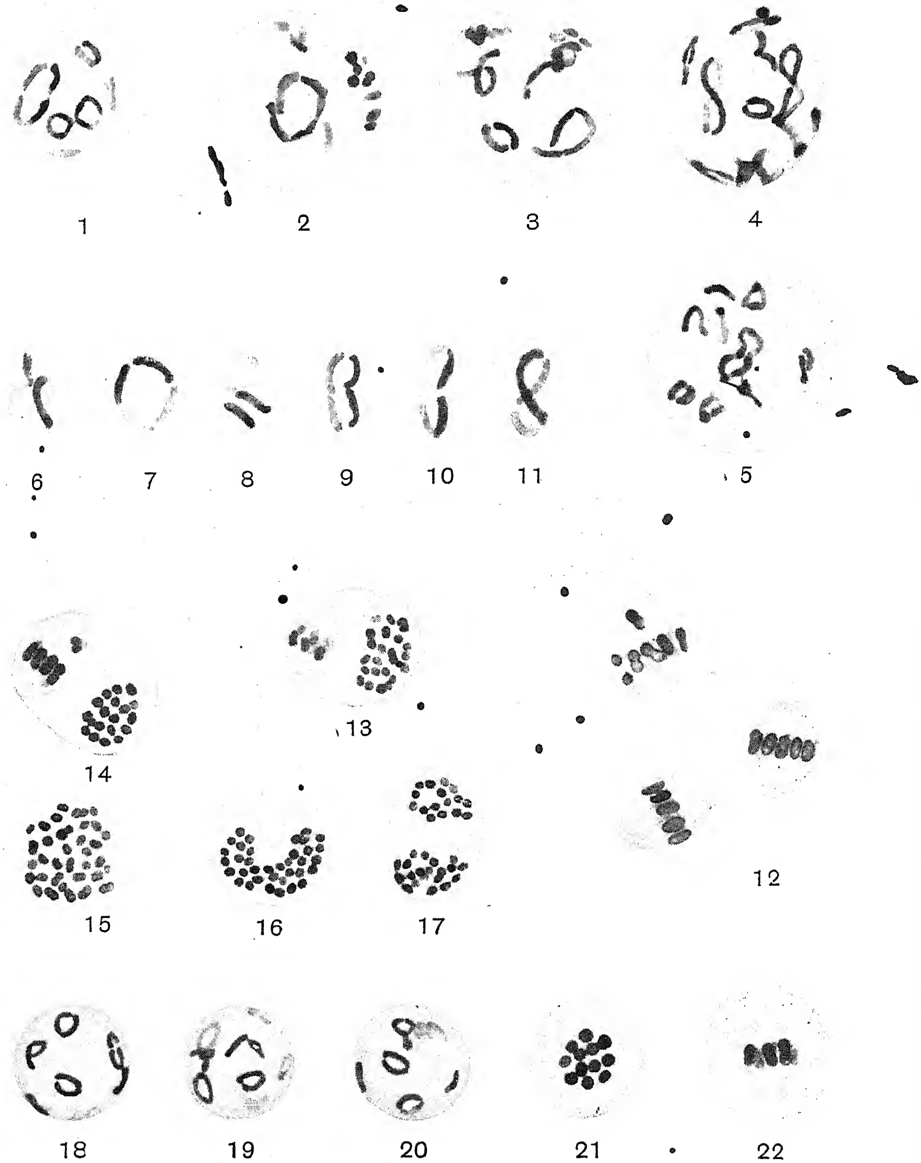
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PLATE XXII.

Figs. 1 and 2. Fern leaf.

Fig. 3. Palmate leaf.

Figs. 4–6. Different phenotypes of the $\mathbf{P_1p_3}$ genotype.

PLATE XXIII.

Tetraploid plant heterozygous in fern leaf ($\mathbf{P_1p_3}$), showing the intermediate leaf type.

PLATE XXIV.

Figs. 1–5. Pollen mother cells from tetraploid *P. sinensis* during diakinesis, showing quadrivalents and bivalents in the same cell.

Figs. 6–11. Different tetrasomic arrangements.

Fig. 12. Metaphases of the first maturation division with one cell, showing irregular distribution of the chromosomes (non-disjunction).

Fig. 13. Equatorial plate from the second maturation division.

Fig. 14. Non-disjunction of chromosomes during the metaphase of the second division.

Fig. 15. Giant equatorial plate from the second division.

Fig. 16. Giant plate formed through fusing of two cells.

Fig. 17. Two equatorial plates from the second division lying in the same plane.

Figs. 18–20. Diakinesis from diploid plant.

Fig. 21. Equatorial plate from metaphase of first division in a diploid plant.

Fi . 22. Spindle from the first division of a diploid plant.

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